For Reference

NOT TO BE TAKEN FROM THIS ROOM

# THE ABSORPTION AND TRANSLOCATION OF NUTRIENTS BY THE WHEAT PLANT

Edwin Kenneth Woodford

Department of Field Crops

University of Alberta

Ex libris
universitatis
albertaensis

Digitized by the Internet Archive
in 2018 with funding from
University of Alberta Libraries

https://archive.org/details/absorptiontransl00edwi

# THE ABSORPTION AND TRANSLOCATION OF NUTRIENTS BY THE WHEAT PLANT

Edwin Kenneth Woodford
Department of Field Crops

A THESIS
submitted to the University of Alberta in
partial fulfilment of the requirements for
the degree of
MASTER OF SCIENCE

Edmonton, Alberta
April 1956

This thesis represents approximately two-thirds of the total work undertaken.

336
#29

## TABLE OF CONTENTS

Page

General introduction ........ 1

Part I. The absorption of nutrients by Reward and Red Bobs grown at Edmonton and Fallis ........ 3

- Introduction ........ 3
- Experimental material ........ 4
- Methods of analysis ........ 8
- Results ........ 10
  - 1. Vegetative parts ........ 10
    - Total weights ........ 12
    - Percentage of dry matter ........ 16
    - Percentage of total ash ........ 21
    - Nitrogen fractions ........ 26
    - Equivalent uptake of anions and cations ........ 27
    - Percentage rate of uptake of plant nutrients ........ 29
  - 2. Straw and grain at maturity ........ 31
    - Total weights ........ 31
    - Percentage of dry matter ........ 36
    - Percentage of total ash ........ 38
    - Quality of grain ........ 39
- Discussion ........ 41
- Conclusions ........ 47

Part II. The distribution of various phosphorus fractions in the developing grain of Reward and Red Bobs grown at Edmonton and Fallis ........ 50

- Introduction ........ 50

TABLE OF CONTENTS (Continued)

Page

Experimental material ........................ 52

Methods of analysis .......................... 54

Results ...................................... 58

Total nitrogen and phosphorus ............ 58

Phosphorus fraction ...................... 61

Percentage of dry matter ............ 61

Percentage of total phosphorus ...... 64

Total weights ....................... 65

Percentage of protein nitrogen ...... 68

The effect of frost on the proportions of phosphorus fractions ...................... 70

Conclusions .................................. 71

Part III. A study of the relationship between nitrate and phosphate absorption using Reward, Red Bobs and Marquis grown in nutrient culture solutions 73

Introduction ................................. 73

Experimental material ........................ 75

Methods of analysis .......................... 78

Results ...................................... 79

General development of plants ........... 79

Chemical analyses ........................ 80

Relationship between nitrate and phosphate absorption ............................... 82

Culture 2 in relation to Fallis soil conditions ............................... 87

Conclusions .................................. 91

## TABLE OF CONTENTS (Continued)

Page

General summary .................................... 92

Acknowledgements ................................... 94

References ......................................... 95

# THE ABSORPTION AND TRANSLOCATION OF NUTRIENTS BY THE WHEAT PLANT

## THE NUTRITION OF REWARD AND RED BOBS GROWN ON THE BLACK AND GRAY SOILS OF ALBERTA IN RELATION TO WHEAT QUALITY

Edwin Kenneth Woodford

## GENERAL INTRODUCTION

The black and gray soils of Alberta are very different in their chemical composition and in their ability to produce crops of high yield and quality (39). Larger yields of both grain and forage crops are always obtained from the black soil, but the differences in the composition of these crops and those grown on the gray soil cannot be explained by the known differences in soil composition.

Experiments (1) with many varieties of wheat have shown that there are marked differences in the composition and quality of the grain grown on the two soils. Wheat grown on the gray soil is inferior in quality to the same variety grown on the black soil, and in addition the flour milled from many of the

varieties deteriorates rapidly on storage and is unfit for commercial bread making purposes after one year. The flour from the same varieties grown on the black soil, however, can be stored for two years without any marked deterioration of the baking quality.

The results reported in this paper are studies of the nutrition of two representative wheat varieties grown at Edmonton in the black and Fallis in the gray soil areas. It was thought that there might be some definite differences in the absorption and translocation of nutrients which could possibly be related to the very marked differences obtained in the original quality and keeping properties of the flour milled from these two wheats grown on the two soils.

The paper is divided into three parts. The first part, which is the most comprehensive and is the basis for further investigations, is a study of the general absorption of nutrients by Reward and Red Bobs grown on the black and gray soils. The second part is a study of nitrogen, phosphorus and phosphorus fractions in the developing grain of the same two varieties grown under the same conditions. The third part is a study of the relationship between nitrate and phosphate absorption by means of nutrient culture solutions.

# PART I

## The Absorption of Nutrients by Reward and Red Bobs Grown at Edmonton and Fallis in Relation to Wheat Quality

### Introduction

It has been demonstrated by many workers that wheat quality is directly affected by the nutrition of the whole plant, and it seems that only by combining the studies of the plant physiologist with those of the cereal chemist will it be possible to solve many of the problems underlying wheat quality. A thorough understanding of the amounts and distribution of the principal nutrients in the wheat plant appeared to be an essential preliminary to the study of the detailed physiological processes which might be responsible for the differences in quality and keeping properties of the flour. It was decided, therefore, to study the absorption and distribution of nutrients in two representative varieties of wheat grown on the black and gray soils at Edmonton and Fallis.

The progressive changes in the chemical composition of the developing wheat plant have been followed by many workers, and results from various parts of the world are available. The work of Knowles and Watkins (13) in

England is the most comprehensive of recent years. The primary object of all these experiments has been to follow the development of the wheat plant and not to study any changes in composition that might result from soil and varietal differences. Recent work reported from French experimental stations (6,18,19,30) on the chemical composition of different varieties grown on different soils has shown the magnitude of some of the changes which may be expected. These studies have, however, been made at only one or two stages in the plant's development, and as far as the writer is aware there is no comprehensive work covering this question over the whole life period of the wheat plant.

The particular varieties used in this study were chosen because they exhibited differences not only in original quality, but also in keeping properties of the flours milled from them. The experiment was designed so that the significance of the differences in varietal and soil reaction might be determined by accepted statistical methods. The question of quality is only briefly mentioned because the gap between the results of this study and those of actual quality determinations is still wide.

## Experimental Material

The material used in this study was grown on fallowed land during the spring and summer of 1934. The experimental plots maintained at Edmonton are typical of

the black, and those at Fallis, of the gray, soil areas. Edmonton and Fallis are 50 miles apart, but are characterized by similar climatic conditions. The rainfall is probably slightly higher at Fallis, but no meteorological data are available. Since the growing of legumes on the gray soil has been shown to affect the yield and composition of subsequent crops, soil which had never grown legumes was selected for this experiment.

The composition of the two soil types is described by Wyatt and Newton (39) who state that the greatest differences occur in the first foot, where the black soil contains about four times as much nitrogen and more than twice as much phosphorus as the gray soil. There are likewise greater quantities of nitrogen, phosphorus, calcium and magnesium in the second and third foot depths of the black soil than in the corresponding depths of the gray soil.

Two varieties of wheat, Reward and Red Bobs, were grown. Reward was chosen because when grown on the gray soil it had the highest quality of all varieties previously tested, and in addition was the only standard variety commonly grown in this area which produced flour which did not deteriorate rapidly on storage. Red Bobs when grown on the gray soil had a marked tendency to produce starchy kernels and yielded a flour with somewhat poorer original quality and decidedly poorer keeping properties. These two varieties are, according to grading standards, equal in quality to Marquis and are eligible for all standard wheat grades.

The experiment was planned to facilitate the statistical analysis of the data. Each variety was replicated eight times on each soil. The varieties were grown side by side in blocks 18 feet long and 12 rows wide. The rows were one foot apart and each variety occupied a sub-block six rows wide. The position of the variety in each block was determined at random. Blocks were adjacent to each other and the whole plot was surrounded by three guard rows.

The plots were sampled five times. Each sample from a sub-block represented the entire length of the block except for a nine inch section at each end which was discarded to remove border effect. The collections were made by a "staircase" method of sampling (Fig. 1). A six inch sample was taken from each row and 27 inches were left between the samples in adjacent rows. The rows in each sub-block and each six inch section in a row were numbered. The starting row and the position of the sample in that row were randomized by the use of Tippet's (33) random sampling numbers. Randomization for all the collections was made at the same time and if overlapping occurred, the starting point in the row was moved so that two samples were never taken from adjacent six inch sections. In this way adjacent samples were nover closer than six inches.

Edmonton plants were cut at the ground level and immediately transferred to the laboratory for chemical analyses. Fallis plants were dug from the soil and all the

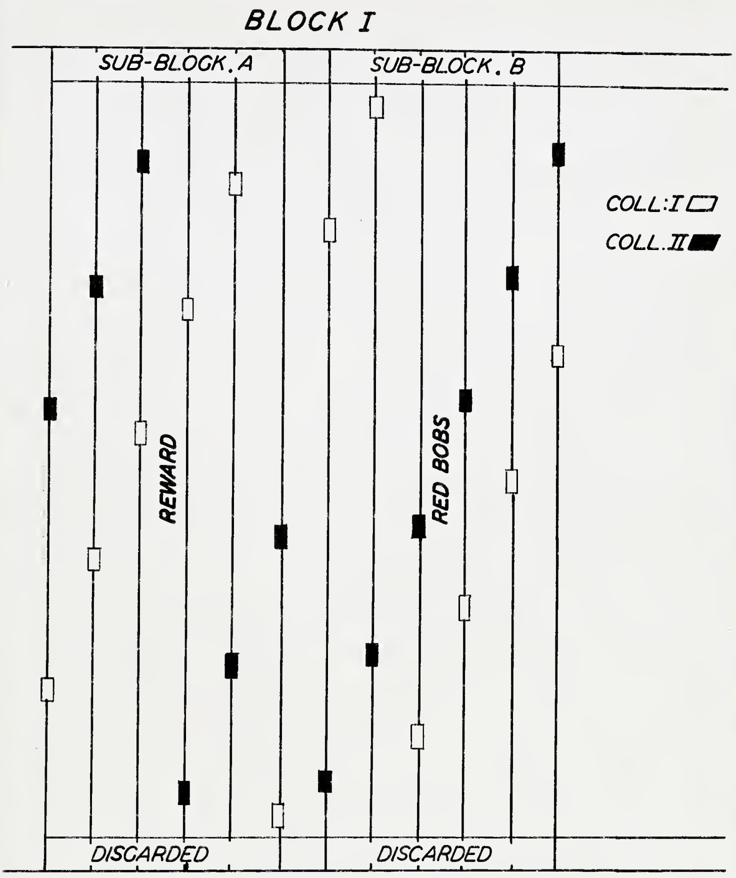


Fig. 1. Diagram of a section of plot and the method of sampling for the first and second collection.

plants from a sub-block transferred to an individual container. In this manner the plants, with roots well covered with soil, were prevented from drying out while they were transported to the laboratory where the tops were cut off just above the ground level immediately prior to analysis.

Comparable collections were made when the plants were at approximately the same stage of development. Five samplings were made as indicated below.

| Collection | Date of collection |  | Days from seeding |  |
|---|---|---|---|---|
|  | Edmonton | Fallis | Edmonton | Fallis |
| 1 | June 6 | June 7 | 29 | 29 |
| 2 | June 26 | June 27 | 48 | 48 |
| 3 | July 11 | July 12 | 64 | 64 |
| 4 | Aug. 13 | Aug. 7 | 97 | 90 |
| 5 | Aug. 31 | Aug. 31 | 115 | 114 |

Collection 3 was made when the plants were fully headed, Collection 4 when the grain contained about 45% moisture and Collection 5 at maturity. The heads and straw and grain and straw of Collections 4 and 5, respectively, were analysed separately.

## Methods of Analysis

The following determinations were made on each of the eight replicates of each variety grown at Edmonton and Fallis.

Dry Matter: - The smaller samples of Collections 1 and 2 were dried directly in a 100°C. air oven. The

larger samples of the later collections were rapidly dried in a blast oven at 75°C., then ground in a Wiley mill and further dried at 100°C.

Total Nitrogen: - Total nitrogen in the vegetative parts was determined by the reduced iron method of Pulcher et al (26) in order to include any nitrate nitrogen which was present. Since it has been shown that nitrate nitrogen if present at all in the grain is negligible, the Kjeldahl method with mercuric oxide as a catalyst was used to determine nitrogen in the grain.

Non-protein Nitrogen: - The fresh green material, ground as finely as possible in a food chopper, was extracted with 2.5% trichloracetic acid, and the total nitrogen of this extract determined by the reduced iron method. The procedure was essentially that used by McCalla (20).

Ash: - Approximately 2 gm. samples of the ground straw and 5 gm. samples of the grain were ashed in a muffle furnace at 650°C. for six hours. The ash was taken up in hot dilute hydrochloric acid and the solution diluted to 100 cc. Aliquots of this solution were used in the determination of all the mineral elements studied except sulphur.

Phosphorus: - Phosphorus was determined using the colorimetric method described by Truog and Meyer (34) and is reported as $P_2O_5$.

Sulphur: - Total sulphur was determined only on a composite sample of each variety at each place.

Approximately 1.5 gm. of the straw and 0.75 gm. of the grain were fused in a Parr heat ignition bomb with 12 gm. of sodium peroxide and 0.5 gm. of zinc. The fused mass was dissolved in hot water, made slightly acid, and then filtered. The sulphate was precipitated as barium sulphate and weighed directly. The procedure was an adaptation of the method described by Wolkoff (35). Total sulphur is reported as $SO_4$.

Potassium: - Potassium was precipitated with sodium cobaltic nitrite and the precipitate titrated with N/20 potassium permanganate. The details of the procedure are described by Hibbard and Stout (12).

Calcium: - Calcium was precipitated as the oxalate and titrated with N/20 potassium permanganate.

Magnesium: - Magnesium in the filtrate from the calcium determination was precipitated as magnesium ammonium phosphate, dissolved in N/14 sulphuric acid and the excess titrated with N/14 sodium hydroxide using methyl red as an indicator.

## Results

The results of the chemical analyses of the developing plants are expressed, first, as the total weight of the individual nutrients absorbed up to the time of each collection; second, as a percentage of dry matter; and third, as a percentage of total ash. The individual

results for each sub-block were too numerous for presentation. The total weights and the mean percentages are presented in graphical form and also in tables with accompanying "t" values which indicate the significance of the differences due to soil and variety.

The test for significance employed throughout is that of "Student" as described by Fisher (8). The experiment provided eight replicate determinations for each variety at each place. These are taken as providing eight replicate determinations of the differences between Reward and Red Bobs at Edmonton and Fallis. The average of the eight individual differences provided an estimate of the mean difference and their variance the basis of testing (a) whether the mean difference at either place differed significantly from zero (i.e. whether there was any real difference between the varieties) and (b) whether the differences between the varieties were the same at Edmonton and Fallis. In a similar manner by the use of totals instead of differences it was determined whether the general level of the various constituents was significantly higher at either Edmonton or Fallis.

These three sets of calculations were made for most of the data and the computed "t" values are listed in Tables I, II, III, IV and VII, together with the total weights or means of the various determinations. The first column of "t" values indicates the significance of the difference in the general level at Edmonton and Fallis. The value for the Fallis sample was always subtracted from

the value for the Edmonton sample, and in consequence a negative sign means that the general level was higher at Fallis. The second and third columns of "t" values indicate the significance of the differences between varieties at Edmonton and Fallis, a negative sign meaning that the weight or percentage was higher in Red Bobs than in Reward. The fourth column of "t" values shows the significance of the difference between the varietal reactions, a high "t" value indicating that the differences between the varieties were not the same at Edmonton as at Fallis.

## Total Weights.

The total weights of dry matter, nitrogen, ash and ash constituents are shown in Fig. 2. In the graphs each point, except for sulphur, represents the total of eight replicate samples. The numerical values for these results, together with "t" values indicating the significance of the differences due to soil and variety, are shown in Table I. Sulphur was determined only on a composite sample from each collection; thus it was impossible to use these data for statistical analysis.

The quantities represented indicate the absorption of the various nutrients from a definite area of soil (48 six inch sections) and a comparison of the curves indicates the fertility of the two soils and the ability of the two varieties to grow on them.

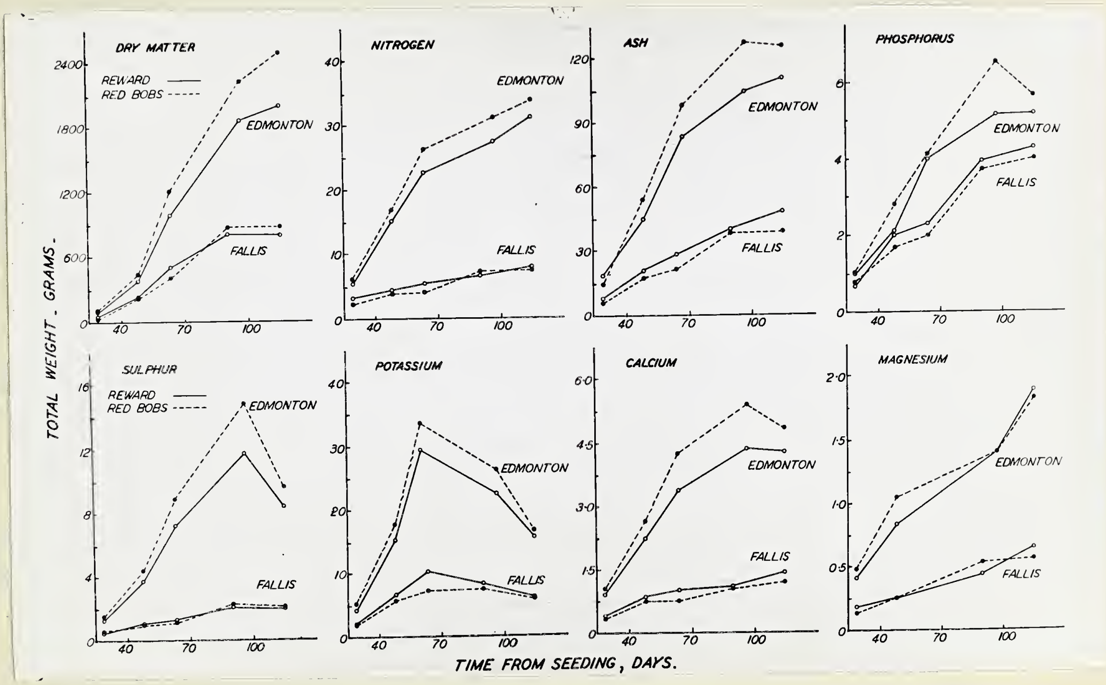


Fig. 2. Total weights of dry matter, nitrogen, ash and ash constituents absorbed by Reward and Red Bobs from a unit area of soil.

TABLE I

Total weights and the significance of differences due to soil and variety

| Determination | Collection | Total weight, gm. | | | | "t" values | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Edmonton | | Fallis | | Difference between general levels at Edmonton and Fallis | Difference between varieties+ | | Difference between varietal reactions at Edmonton and Fallis |
| | | Reward | Red Bobs | Reward | Red Bobs | | Edmonton | Fallis | |
| Dry matter | 1 | 100.6 | 122.5 | 59.4 | 53.9 | 7.11** | -3.12** | 0.85 | 2.81* |
| | 2 | 380.0 | 443.4 | 236.5 | 233.0 | 5.57** | -1.60 | 0.05 | 1.17 |
| | 3 | 990.4 | 1223.7 | 501.2 | 406.7 | 25.37** | -4.17** | 1.68 | 4.52** |
| | 4 | 1863.4 | 2357.8 | 814.0 | 884.3 | 11.51** | -0.43 | 0.05 | 0.34 |
| | 5 | 2011.4 | 2487.1 | 827.9 | 884.6 | 21.08** | -0.64 | -0.46 | 0.07 |
| Nitrogen | 1 | 5.77 | 6.74 | 3.11 | 2.81 | 8.21** | -2.30* | 0.74 | 2.16* |
| | 2 | 15.43 | 17.07 | 4.68 | 4.15 | 17.35** | -1.13 | 0.34 | 1.89 |
| | 3 | 22.98 | 26.43 | 5.61 | 4.27 | 19.30** | -4.56** | 1.68 | 4.41** |
| | 4 | 27.53 | 31.50 | 6.99 | 7.54 | 18.52** | -2.40* | -0.32 | 1.47 |
| | 5 | 31.04 | 34.43 | 8.18 | 7.79 | 16.07** | 1.76 | 0.03 | 1.23 |
| Ash | 1 | 18.81 | 15.01 | 8.38 | 6.90 | 9.09** | -1.00 | 1.59 | 1.83 |
| | 2 | 46.74 | 54.54 | 20.81 | 18.17 | 12.59** | -2.63* | 1.18 | 2.69* |
| | 3 | 85.27 | 99.61 | 29.47 | 22.49 | 13.86** | -5.01** | 2.72* | 5.47** |
| | 4 | 106.48 | 128.63 | 41.32 | 40.71 | 11.50** | 1.16 | 0.95 | 0.14 |
| | 5 | 112.17 | 124.04 | 49.78 | 40.02 | 11.32** | -2.28* | 0.10 | 1.69 |
| Phosphorus $(P_2O_5)$ | 1 | 1.02 | 1.04 | 0.67 | 0.72 | 2.81* | -0.77 | -0.46 | 0.22 |
| | 2 | 2.28 | 2.71 | 2.13 | 1.70 | 0.93 | -1.65 | 1.21 | 2.02 |
| | 3 | 3.96 | 4.16 | 2.71 | 2.07 | 6.53** | -0.54 | 2.08 | 1.85 |
| | 4 | 5.19 | 6.69 | 3.98 | 3.71 | 17.28** | -2.73* | 0.44 | 2.24** |
| | 5 | 5.31 | 5.86 | 4.24 | 4.04 | 2.73* | 0.94 | -0.01 | 0.67 |
| Potassium | 1 | 4.52 | 5.23 | 2.16 | 2.02 | 7.12** | -1.29 | -0.47 | 0.58 |
| | 2 | 15.58 | 17.96 | 6.86 | 5.90 | 11.63** | -1.84 | 0.75 | 1.83 |
| | 3 | 29.61 | 33.90 | 10.32 | 7.24 | 12.24** | -3.23** | 1.95 | 3.66** |
| | 4 | 22.48 | 26.34 | 8.56 | 7.79 | 13.43** | -2.03 | 0.40 | 1.72 |
| | 5 | 15.80 | 19.93 | 6.25 | 5.70 | 11.41** | -0.80 | 0.32 | 0.79 |
| Calcium | 1 | 0.91 | 1.09 | 0.43 | 0.38 | 10.57** | -3.21** | 0.86 | 2.88* |
| | 2 | 2.24 | 2.66 | 0.87 | 0.77 | 15.92** | -1.88 | 0.28 | 1.53 |
| | 3 | 3.37 | 4.28 | 1.00 | 0.77 | 12.47** | -6.47** | 2.04 | 6.01** |
| | 4 | 4.37 | 5.50 | 1.11 | 1.10 | 17.83** | -3.76** | 0.00 | 2.66* |
| | 5 | 4.30 | 4.86 | 1.44 | 1.24 | 13.03** | 0.85 | 0.62 | 0.16 |
| Magnesium | 1 | 0.42 | 0.48 | 0.18 | 0.14 | 11.30** | -1.62 | 1.37 | 2.11 |
| | 2 | 0.84 | 1.06 | 0.26 | 0.26 | 13.92** | -2.45* | 0.28 | 1.93 |
| | 4 | 1.42 | 1.42 | 0.44 | 0.53 | 12.45** | 0.35 | -0.42 | 0.55 |
| | 5 | 1.84 | 1.77 | 0.66 | 0.56 | 12.63** | 1.92 | 0.63 | 0.92 |

+ A minus sign indicates that the weight for Red Bobs is higher than for Reward.
* 5% point, t = 2.15.
** 1% point, t = 2.98.

The figures show that at every collection the weights of dry matter and all other constituents determined were higher for Edmonton than for Fallis samples. The magnitude of these differences for all constituents, except potassium and sulphur, increased with the age of the plant. These elements were excreted from the plants and the greatest differences in weights occurred before excretion had started, at Collection 3 for potassium and Collection 4 for sulphur. At the point of the maximum difference the quantities of nitrogen, ash, sulphur, potassium and calcium in the Edmonton plants were approximately four times as high as in the Fallis plants. Phosphorus was exceptional; the differences between Edmonton and Fallis samples were much smaller throughout the growth period and were insignificant in Collection 2. This proportionately greater absorption of phosphorus cannot be attributed to the amount of phosphorus in the gray soil which is only 60% of that present in black soil. Nor can it be attributed to the greater amount of phosphorus in relation to the other elements. In relation to calcium and magnesium, phosphorus is less in the gray soil than in the black.

The differences between varieties were significant (5% point) for only one determination in the Fallis samples, but for more than one-third of the determinations in the Edmonton samples. Thus the results show that Red Bobs absorbed more nutrients than Reward at Edmonton and less at Fallis, but that this difference was significant for less than one-third of the determinations.

## Percentage Data.

Dry Matter as a Percentage of Green Weight: - The percentages of dry matter in the fresh samples of the first four collections are shown in the top left hand graph of Fig. 3. The numerical values of these results, together with "t" values indicating the significance of the differences due to soil and variety, are shown in Table II. Collection 5 is not considered as it was made after the plants were mature.

Fallis samples were definitely higher in dry matter content than corresponding Edmonton samples.

Red Bobs was higher than Reward in percentage of dry matter for both Edmonton and Fallis plants, and this difference was significant in all but Collections 2 and 3 at Edmonton.

Dry matter content is often used as an indication of the stage of maturity of the plant. The percentage of dry matter was higher in the Fallis than in the Edmonton plants, and indicated that the Fallis samples were more mature than the Edmonton samples. The individual collections were therefore not strictly comparable, and it might have been better to have plotted all other data against the percentage of dry matter, rather than against the number of days from seeding. This would not, however, have altered the general appearance of the graphs nor any conclusions drawn from them. In this regard it is pointed out that Red Bobs is a later maturing variety on both soils,

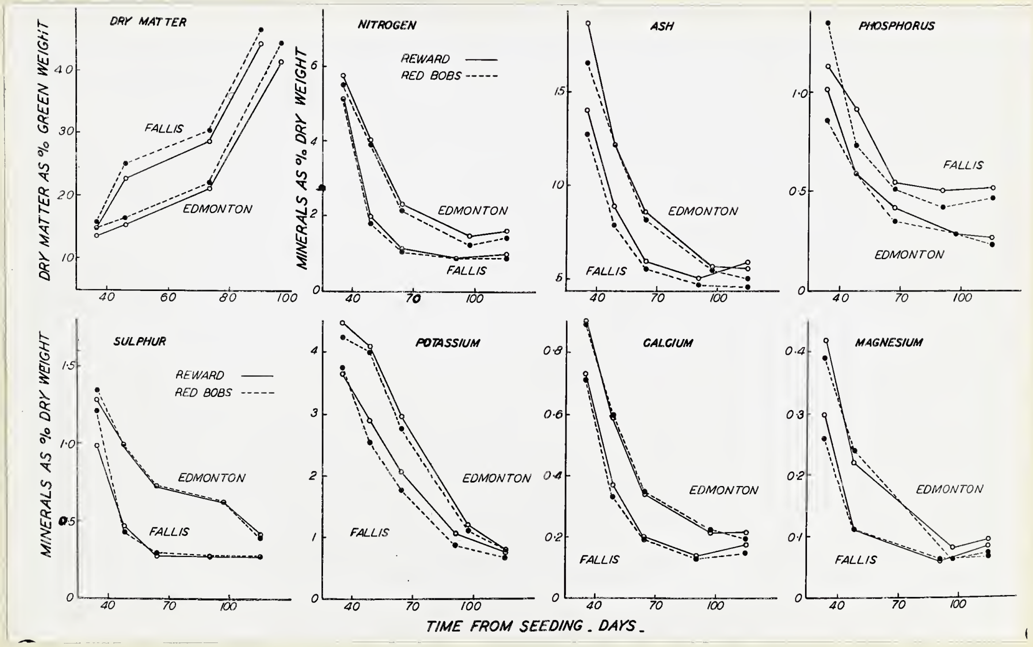


Fig. 3. Dry matter as a percentage of green weight; nitrogen, ash and ash constituents as a percentage of dry matter in Reward and Red Bobs plants at progressive stages of maturity.

TABLE II

Percentage data and the significance of differences due to soil and variety

| Determination | Collection | Mean of 8 replicate samples | | | | "t" values | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Edmonton | | Fallis | | Difference between general levels+ at Edmonton and Fallis | Difference between varieties++ | | Difference between varietal reactions at Edmonton and Fallis |
| | | Reward | Red Bobs | Reward | Red Bobs | | Edmonton | Fallis | |
| Dry matter, % green weight | 1 | 13.4 | 14.6 | 14.8 | 15.5 | -2.94* | -6.89** | -4.05** | 2.01 |
| | 2 | 15.3 | 16.3 | 22.8 | 25.1 | -9.13** | -1.35 | -3.44** | 1.47 |
| | 3 | 21.2 | 22.2 | 28.8 | 30.4 | -4.33** | -1.82 | -3.13** | 0.92 |
| | 4 | 41.8 | 44.8 | 44.3 | 46.7 | -2.87* | -3.43** | -2.78* | 0.46 |
| Nitrogen, % dry matter | 1 | 5.74 | 5.50 | 5.24 | 5.22 | 6.55** | 3.80** | -0.05 | 2.90* |
| | 2 | 4.06 | 3.85 | 1.98 | 1.78 | 9.36** | 2.91* | 3.64** | 0.52 |
| | 3 | 2.32 | 2.16 | 1.12 | 1.05 | 12.36** | 3.15** | 1.29 | 1.32 |
| | 4 | 1.48 | 1.33 | 0.86 | 0.85 | 24.97** | 6.86** | 0.39 | 4.61** |
| | 5 | 1.54 | 1.39 | 0.99 | 0.88 | 17.35** | 8.63** | 3.80** | 3.42** |
| Ash, % dry matter | 1 | 18.70 | 16.69 | 14.14 | 12.78 | 12.16** | 5.03** | 3.70** | 0.94 |
| | 2 | 12.28 | 12.30 | 8.84 | 7.80 | 13.45** | 0.38 | 3.71** | 2.35* |
| | 3 | 8.61 | 8.14 | 5.88 | 5.53 | 9.34** | 2.58* | 1.93 | 0.45 |
| | 4 | 5.70 | 5.45 | 5.14 | 4.60 | 3.77** | 1.25 | 2.68* | 1.01 |
| | 5 | 5.50 | 4.93 | 5.88 | 4.51 | 0.12 | 2.03 | 3.99** | 1.39 |
| Phosphorus ($P_2O_5$), % dry matter | 1 | 1.01 | 0.85 | 1.13 | 1.33 | -4.57** | 4.59** | -5.30** | 6.99** |
| | 2 | 0.60 | 0.61 | 0.90 | 0.73 | -2.08 | -0.24 | 3.39** | 2.42* |
| | 3 | 0.40 | 0.34 | 0.54 | 0.51 | -4.80** | 4.55** | 1.95 | 1.84 |
| | 4 | 0.28 | 0.28 | 0.50 | 0.42 | -11.01** | 0.06 | 4.92** | 3.44** |
| | 5 | 0.26 | 0.23 | 0.51 | 0.46 | -8.89** | 1.75 | 2.91* | 0.81 |
| Potassium, % dry matter | 1 | 4.49 | 4.26 | 3.64 | 3.74 | 3.88** | 1.45 | 0.16 | 1.14 |
| | 2 | 4.10 | 4.05 | 2.90 | 2.53 | 12.72** | 0.27 | 2.73* | 1.74 |
| | 3 | 2.99 | 2.77 | 2.06 | 1.78 | 11.51** | 3.08** | 3.51** | 0.30 |
| | 4 | 1.21 | 1.12 | 1.06 | 0.88 | 5.54** | 2.64* | 5.38** | 1.94 |
| | 5 | 0.78 | 0.78 | 0.75 | 0.65 | 2.65* | -0.05 | 3.86** | 2.76* |
| Calcium, % dry matter | 1 | 0.90 | 0.89 | 0.73 | 0.71 | 5.79** | 0.60 | 1.14 | 0.38 |
| | 2 | 0.59 | 0.60 | 0.37 | 0.33 | 9.48** | 0.50 | 1.85 | 1.66 |
| | 3 | 0.34 | 0.35 | 0.20 | 0.19 | 17.95** | -0.93 | 1.24 | 1.53 |
| | 4 | 0.22 | 0.28 | 0.13 | 0.13 | 17.68** | -0.98 | 0.98 | 1.39 |
| | 5 | 0.22 | 0.19 | 0.17 | 0.14 | 8.84** | 2.56* | 3.31** | 0.53 |
| Magnesium, % dry matter | 1 | 0.42 | 0.39 | 0.30 | 0.26 | 9.71** | 1.25 | 1.74 | 0.35 |
| | 2 | 0.22 | 0.24 | 0.11 | 0.11 | 18.22** | -1.39 | 0.56 | 1.37 |
| | 4 | 0.080 | 0.060 | 0.058 | 0.060 | 3.46** | 4.81** | -0.44 | 3.71** |
| | 5 | 0.093 | 0.071 | 0.081 | 0.063 | 2.64* | 2.89* | 2.64* | 0.17 |

+ A minus sign indicates that the percentage is higher in the Fallis plants.
++ A minus sign indicates that the percentage for Red Bobs is higher than for Reward.
* 5% point, t = 2.15.
** 1% point, t = 2.98.

but that it was in every instance higher in the percentage of dry matter than Reward. Thus, in this experiment, the percentage of dry matter in the whole plant did not indicate the stage of the varieties' development, and its use as the abscissa would have been no more justified than that of the number of days from seeding.

Nitrogen, Ash and Ash Constituents as a Percentage of Dry Matter: - The average values for nitrogen, ash and ash constituents expressed as percentages of dry matter are presented graphically in Fig. 3 and numerically in Table II together with "t" values indicating the significance of the differences due to soil and variety.

The general shape of the curves for all constituents in both Edmonton and Fallis samples is similar. The general level of all constituents except phosphorus, was higher in the Edmonton than in the Fallis samples, and was significant in every instance except the percentage of ash in Collection 5. The sulphur results were not analysed statistically, but the graph shows greater differences between the general levels of this element in the Edmonton and Fallis samples than for any other constituent.

The results show that in general the percentage of the constituents in Reward was higher than in Red Bobs for the samples from both soils. This difference was significant in over 50% of the cases and in only one instance, phosphorus in Collection 1 at Fallis, was Red Bobs significantly higher than Reward. The statistical analyses

also show that this difference between Reward and Red Bobs was in general greater at Fallis than at Edmonton. This was not so with the nitrogen results which were significantly higher in all collections of Reward samples at Edmonton, while at Fallis they were significantly higher only in Collections 2 and 5. Thus the difference in the percentage of nitrogen in Reward and Red Bobs was greater at Edmonton, while for all other constituents the difference between varieties was predominantly greater at Fallis. The percentage of nitrogen and sulphur in the Fallis samples fell very rapidly between Collections 1 and 3. The total weight results (Fig. 2) show that during the first month the Fallis plants absorbed approximately 37% of their total nitrogen and 28% of their total sulphur, while the corresponding figures for Edmonton plants were 19% for nitrogen and 12% for sulphur. This indicates that nitrogen and sulphur were readily available throughout the plants' growth at Edmonton, while at Fallis they were readily available only in the early stages and then became limiting. Phosphorus was definitely higher in the Fallis plants, and the percentage of the total uptake of this element absorbed during the first month of growth was 17% at Fallis as compared to 16% at Edmonton, indicating that phosphorus was equally available to the Fallis and the Edmonton plants.

Various workers (11,14,15,25) have shown that there is a reciprocal relationship between the amounts of nitrogen and phosphorus absorbed by the plants and between

the percentages of these elements occurring within the plant. Low nitrogen supply, together with available phosphorus, may then be responsible for the definitely higher concentrations of phosphorus in the Fallis plants.

The importance of sulphur in this connection must also be noted. Marsh (16) showed that a reciprocal relationship also exists between sulphur and phosphorus in the tomato plant. The high concentration of phosphorus in Fallis samples may be due partly to the effect of low nitrogen and partly to the effect of low sulphur.

Ash Constituents as a Percentage of Total Ash. The average values for phosphorus, sulphur, potassium and calcium expressed as percentages of ash are presented graphically (Fig. 4). Table III gives the numerical values for these results, together with accompanying "t" values which indicate the significance of differences due to soil and variety.

Unlike the previous results the graphs for the individual constituents are not similar. Phosphorus as a percentage of the ash remained fairly constant in the samples ~~for~~ from each soil but was almost twice as high in the Fallis samples. The percentage of sulphur in the Edmonton plants rose to a maximum at the time of Collection 4 and then fell as excretion of this element from the vegetative parts of the plant commenced (Fig. 2). The condition in the Fallis samples was very different. The percentage of sulphur decreased until Collection 2 and then remained

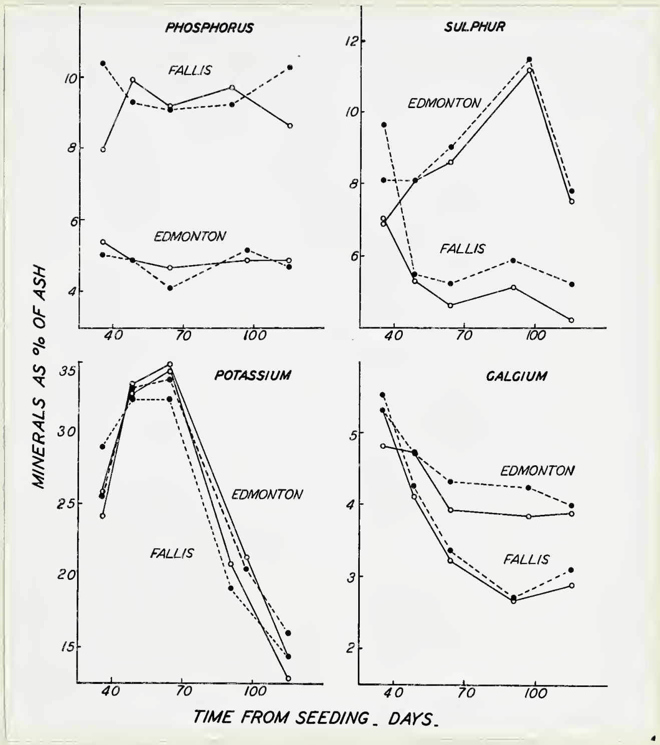


Fig. 4. Ash constituents as a percentage of total ash in Reward and Red Bobs plants at progressive stages of maturity.

TABLE III

Minerals as a percentage of ash and the significance of differences due to soil and variety

| Determination | Collection | Mean of 8 replicate samples | | | | "t" values | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Edmonton | | Fallis | | Difference between general levels+ at Edmonton and Fallis | Difference between varieties++ | | Difference between varietal reactions at Edmonton and Fallis |
| | | Reward | Red Bobs | Reward | Red Bobs | | Edmonton | Fallis | |
| Phosphorus $(P_2O_5)$ | 1 | 5.41 | 5.08 | 7.98 | 10.40 | -13.15** | 1.14 | -8.58** | 6.87** |
| | 2 | 4.87 | 4.93 | 9.70 | 9.26 | -18.90** | -0.16 | 1.05 | 0.86 |
| | 3 | 4.68 | 4.12 | 9.17 | 9.08 | -16.87** | 2.68* | 0.40 | 1.62 |
| | 4 | 4.98 | 5.15 | 9.63 | 9.20 | -15.25** | -0.52 | 1.30 | 1.29 |
| | 5 | 4.83 | 4.73 | 8.60 | 10.27 | - 7.45** | 0.33 | -5.39** | 4.05** |
| Potassium | 1 | 24.2 | 25.5 | 25.9 | 29.2 | - 2.54* | -0.11 | -2.78* | 1.89 |
| | 2 | 33.5 | 33.1 | 32.8 | 32.4 | 0.72 | 0.32 | 0.36 | 0.03 |
| | 3 | 34.8 | 33.9 | 34.4 | 32.3 | 1.38 | 0.98 | 2.50* | 1.07 |
| | 4 | 21.2 | 20.5 | 20.7 | 19.2 | 0.72 | 4.25** | 6.91** | 1.88 |
| | 5 | 14.4 | 16.0 | 12.8 | 14.5 | 1.14 | -2.43* | -2.57* | 0.10 |
| Calcium | 1 | 4.83 | 5.32 | 5.33 | 5.54 | -1.59 | -2.07 | -0.15 | 1.36 |
| | 2 | 4.76 | 4.72 | 4.11 | 4.27 | 6.01** | -0.57 | -1.17 | 0.42 |
| | 3 | 3.91 | 4.32 | 3.22 | 3.38 | 2.61* | -6.80** | -2.63* | 2.95* |
| | 4 | 3.84 | 4.21 | 2.25 | 2.72 | 10.66** | -2.40* | -0.39 | 1.42 |
| | 5 | 3.89 | 3.96 | 2.94 | 3.20 | 7.23** | -0.52 | -1.86 | 0.95 |

+ A minus sign indicates that the percentage is higher in the Fallis plants.
++ A minus sign indicates that the percentage for Red Bobs is higher than for Reward.
* 5% point, t = 2.15.
** 1% point, t = 2.98.

fairly constant. The difference between these two sets of curves is striking, and is further evidence that the amount of sulphur in the Fallis soils limited the plant growth. The potassium content was almost identical for both varieties and soils; it rose to a maximum at the time of Collection 3 and then fell rapidly as excretion of this element began. The calcium curves are somewhat similar for the samples from both soils. In the Fallis plants there was a more rapid decrease in the percentage of calcium which was followed, at the time of the last collection, by a definite increase not apparent in the Edmonton plants. It is shown in a later section of this paper that this increase was definitely reflected in the composition of the grain.

The results in Table III show that the percentage of phosphorus in the ash was definitely higher in Fallis samples at all stages, that calcium was higher for the last four collections at Edmonton, and that potassium was higher for Collection 1 at Fallis but almost the same for all others.

There were no consistent significant differences between the varieties when grown on the same soil, although the results indicate that the ash percentage of Red Bobs was higher in sulphur and calcium than that of Reward for both Edmonton and Fallis samples. Likewise there were no consistent significant differences between the reactions of the varieties to the two soils.

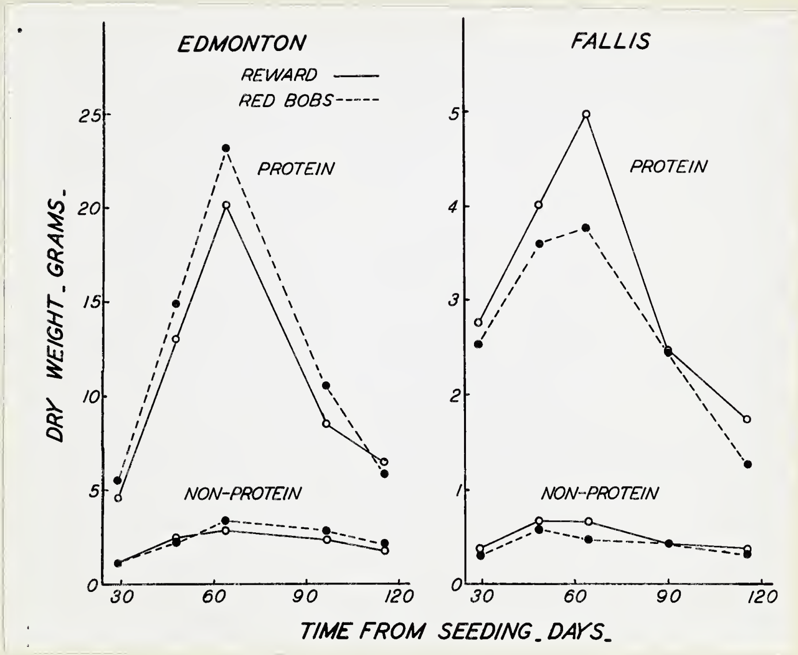


Fig. 5. Total weights of protein and non-protein nitrogen in the vegetative parts of Reward and Red Bobs from a unit area of soil.

## Nitrogen Fractions.

Total nitrogen was separated into protein and organic non-protein fractions. Nitrate nitrogen was also determined in Collection 1, but this fraction was less than 1% of the total nitrogen and is not considered.

The total weights of protein and non-protein nitrogen in the vegetative parts of all collections of Edmonton and Fallis plants are represented graphically in Fig. 5. Although the total weights in Edmonton samples were nearly five times those of Fallis samples, the relative changes in the amounts of total protein and non-protein nitrogen were in general the same at both places. The weights of both fractions rose to a maximum at the time of Collection 3, when heading was almost complete, and then fell until maturity.

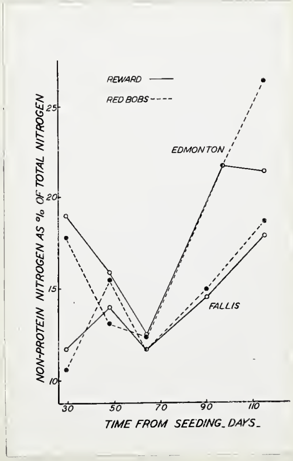


Fig. 6. Non-protein nitrogen as a percentage of total nitrogen in the vegetative parts.

Non-protein as a percentage of the total nitrogen in the vegetative parts is shown in Fig. 6. At the time of Collections 2 and 3 this fraction was much the same for both Edmonton and Fallis samples. When translocation of nitrogen to the grain began, a relatively larger proportion of the nitrogen in the vegetative parts of the Edmonton plants was non-protein. If the results of water culture experiments (20) are applicable to studies carried out in the field, this higher proportion of non-protein nitrogen was the result of a higher absorption of nitrogen during the later stages of growth. The total weight results (Fig. 1) show that the absorption of nitrogen by the Edmonton plants after Collection 3 was on the average 8 gm. as compared with an average of 3 gm. for the Fallis plants. These results may be taken as additional evidence that nitrogen was limiting general development and metabolism under Fallis conditions.

## Equivalent Uptake of Anions and Cations.

The results so far discussed lead to the general conclusion that phosphorus is relatively more available than nitrogen and sulphur in the Fallis soil. The importance of this relationship in altering the composition of the plant is shown in Fig. 7, where the ratios of nitrogen:phosphorus and sulphur:phosphorus in the plants at the various collections are plotted. The ratios are calculated from the equivalent weights of the elements,

and the graphs show that both of these ratios were definitely higher at all times in the Edmonton plants. This was to be expected if nitrogen and sulphur were limiting at Fallis while phosphorus was readily available.

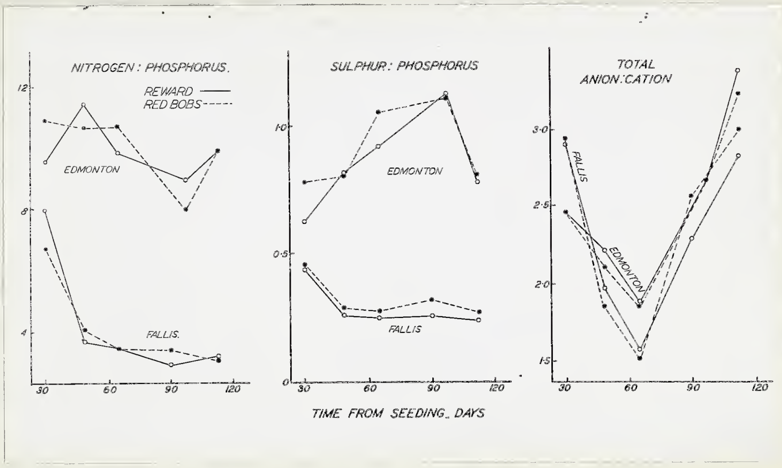


Fig. 7. Ratios of the equivalent uptake of nitrogen and phosphorus, sulphur and phosphorus and total anions:cations in Reward and Red Bobs at progressive stages of maturity.

It has already been suggested that the Fallis plants absorbed large amounts of phosphorus to compensate for the low availability of nitrogen and sulphur. If this reciprocal nature of the anions, nitrogen, sulphur and phosphorus did in some way tend to control the total amount of anions absorbed, then there should be a fairly constant relationship between the principal anions and cations absorbed from each soil. This anion:cation ratio was calculated in terms of equivalents for the two varieties for all collections and is also shown graphically in Fig. 7.

The curves show that the ratio was highest in the early stages of the plants' growth, fell gradually until Collection 3 and then, due to the excretion of potassium, increased until the plants were mature. The curves for both varieties and soils are similar and substantiate the hypothesis that there is a controlling influence which regulates the proportion of anions to cations absorbed despite the limiting supply of two of the anions. The high phosphorus content in the Fallis plants was probably not due to the greater availability of phosphorus at Fallis but rather to the influence controlling the anion:cation balance.

## Percentage Rate of Uptake of Plant Nutrients.

Besides the differences in total amounts of nutrients absorbed from the two soils there was a marked difference in the rates of nutrient uptake between collections. It has already been noted that the amounts of nitrogen and sulphur absorbed during the first month of growth was proportionately much greater at Fallis. To illustrate this difference in the rate of uptake the average percentage absorption between collections was calculated. The weight of an element absorbed between successive collections was divided by the number of days between the collections, and this value expressed as a percentage of the total amount of the element absorbed. These percentages

for nitrogen, phosphorus, sulphur and potassium in Reward grown on both soils are plotted against days from seeding in Fig. 8. The data of this experiment are somewhat inadequate for this type of calculation, but the general shape of the curves clearly demonstrates the point in question.

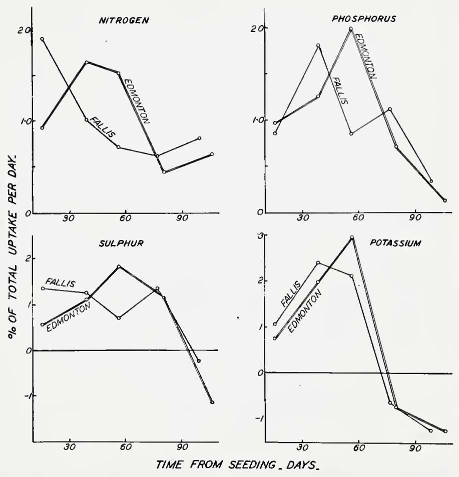


Fig. 8. The percentage rate of uptake of nutrients by Reward at progressive stages of maturity.

The graphs show that the rate of nitrogen absorption at Edmonton increased until Collection 3, while at Fallis the rate decreased from Collection 1 to Collection 4. The graph for sulphur shows a somewhat similar relationship between the percentage rates at the two places. The phosphorus and potassium curves are more nearly alike for Edmonton and Fallis plants. The rise and fall in the percentage rate of absorption of potassium was very

similar for the two places, while the only marked difference in the percentage rate of absorption of phosphorus was between Collections 2 and 3. The percentage rate of absorption of each of the four elements reached a maximum between Collections 2 and 3 at Edmonton, but at Fallis this rate of absorption for nitrogen and sulphur was at a maximum before Collection 1. The lower percentage rate of absorption of nitrogen and sulphur by Fallis plants can only be attributed to the low availability of these two elements in the gray soil.

## Composition of Straw and Grain at Maturity

### Total Weights.

The total weights of dry matter, nitrogen, ash and ash constituents in grain and straw of mature plants are shown as bar diagrams in Fig. 9. These weights are also recorded in Table IV, together with the "t" values indicating the significance of the differences due to soil and variety.

The figures show clearly the differences in the amount of nutrients absorbed at the two places and the manner of their distribution between straw and grain. The weights of all constituents were definitely higher in the Edmonton plants. There was, however, no significant difference between the weights of phosphorus in the straw and calcium in the grain. Differences between varieties are

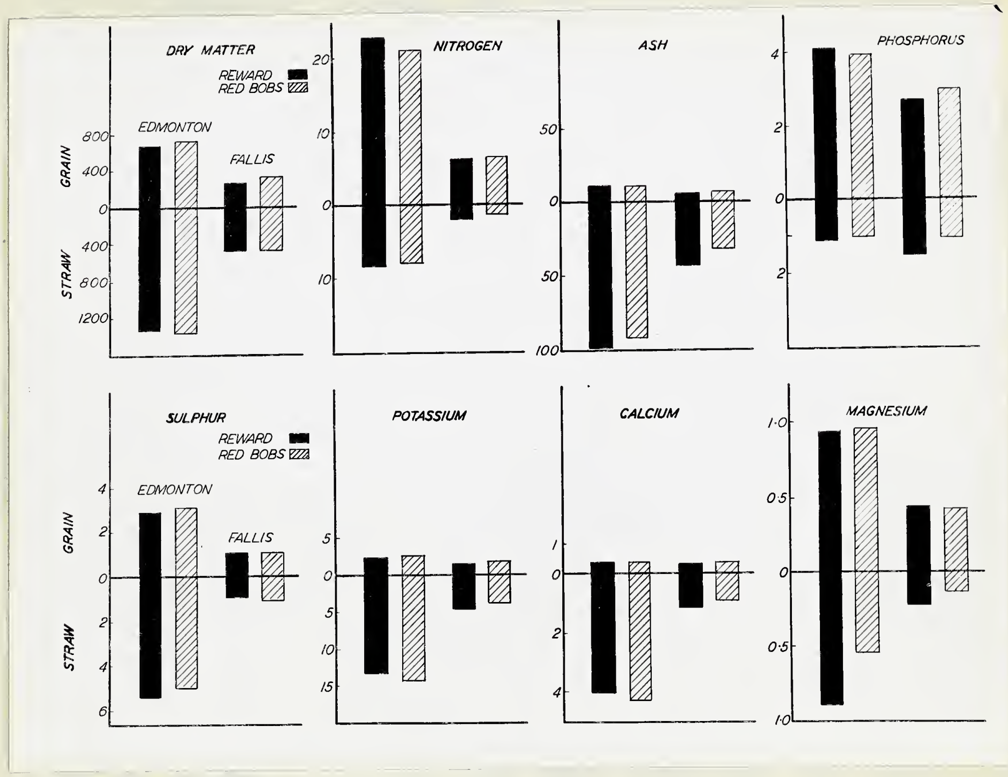


Fig. 9. Total weights of dry matter, nitrogen, ash and ash constituents in grain and straw of the final collection.

## TABLE IV

Total weights in straw and grain of mature plants and the significance of differences due to soil and variety

| Determination | Part of plant | Total weight, gm. | | | | "t" values | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Edmonton | | Fallis | | Difference between general levels[+] at Edmonton and Fallis | Difference between varieties[++] | | Difference between varietal reaction at Edmonton and Fallis |
| | | Reward | Red Bobs | Reward | Red Bobs | | Edmonton | Fallis | |
| Dry matter | Grain | 675.1 | 728.6 | 263.6 | 324.3 | 10.24** | -1.35 | -1.55 | 0.14 |
| | Straw | 1336.3 | 1362.0 | 564.0 | 560.0 | 19.55** | -0.30 | 0.04 | 0.24 |
| Nitrogen | Grain | 22.75 | 21.06 | 6.09 | 6.19 | 16.00** | 1.74 | -0.02 | 1.24 |
| | Straw | 8.29 | 8.04 | 2.09 | 1.60 | 10.98** | 0.69 | -0.55 | 0.10 |
| Ash | Grain | 11.68 | 11.95 | 5.48 | 6.29 | 10.80** | -0.02 | -0.27 | 0.20 |
| | Straw | 100.49 | 92.90 | 44.30 | 33.73 | 10.69** | 1.41 | 1.46 | 0.00 |
| Phosphorus ($P_2O_5$) | Grain | 4.15 | 3.89 | 2.66 | 2.95 | 4.00** | 0.06 | -0.97 | 1.10 |
| | Straw | 1.16 | 1.06 | 1.58 | 1.09 | -1.28 | 0.16 | 3.10** | 2.08 |
| Potassium | Grain | 2.30 | 2.55 | 1.40 | 1.72 | 4.61** | -1.52 | -1.71 | 0.14 |
| | Straw | 13.50 | 14.30 | 4.85 | 3.98 | 22.42** | -0.67 | 0.83 | 1.05 |
| Calcium | Grain | 0.28 | 0.29 | 0.26 | 0.29 | 0.32 | 0.03 | 1.13 | 0.77 |
| | Straw | 4.01 | 4.60 | 1.19 | 0.95 | 13.75** | 0.92 | 0.84 | 0.06 |
| Magnesium | Grain | 0.95 | 0.95 | 0.44 | 0.42 | 9.37** | -0.23 | 0.19 | 0.29 |
| | Straw | 0.90 | 0.55 | 0.22 | 0.14 | 9.70** | 2.52* | 0.77 | 1.26 |

[+] A minus sign means the weight is higher for Fallis plants.
[++] A minus sign means the weight is higher in Red Bobs than Reward.
[*] 5% point, t = 2.15.
[**] 1% point, t = 2.98.

significant in only two instances; at Edmonton magnesium was higher, while at Fallis phosphorus was higher, in the straw of Reward plants.

The percentages of nutrients translocated to the grain are shown in Table V. There was a much greater percentage translocation of nitrogen, phosphorus and magnesium than of any of the other constituents. The percentage of all nutrients translocated to the grain of Edmonton plants was approximately the same for Reward as for Red Bobs. At Fallis the tendency was for Red Bobs to produce more grain in comparison with ~~to~~ total plant than Reward, and there was a correspondingly greater translocation of all nutrients except phosphorus.

TABLE V

The weight of dry matter, ash and nutrients in the grain at maturity expressed as a percentage of the total in the whole plant

| Collection | Dry matter | Nitrogen | Ash | Phosphorus | Sulphur | Potassium | Calcium | Magnesium |
|---|---|---|---|---|---|---|---|---|
| Edmonton | | | | | | | | |
| Reward | 33.6 | 73.2 | 10.4 | 78.2 | 34.6 | 14.6 | 6.6 | 51.4 |
| Red Bobs | 34.8 | 72.4 | 11.4 | 78.5 | 32.3 | 15.1 | 6.7 | 63.6 |
| Fallis | | | | | | | | |
| Reward | 31.8 | 74.4 | 11.0 | 62.7 | 58.9 | 22.4 | 17.9 | 65.9 |
| Red Bobs | 36.7 | 79.5 | 15.7 | 73.0 | 53.7 | 30.2 | 23.1 | 75.0 |

Total weights of dry matter and nutrients in 1000 kernels are shown in Table VI. The weight of nitrogen was

## TABLE VI

Weight of dry matter and nutrients per 1000 kernels, and their relation to nitrogen

| Sample | | Dry matter | Nitrogen | Ash | Phosphorus | Sulphur | Potassium | Calcium | Magnesium |
|---|---|---|---|---|---|---|---|---|---|
| Wt. of 1000 kernels | | | | | | | | | |
| Edmonton | Reward | 26.3 | 1.007 | 0.357 | 0.184 | 0.129 | 0.102 | 0.0126 | 0.0419 |
| | Red Bobs | 26.7 | 0.876 | 0.456 | 0.162 | 0.130 | 0.106 | 0.0121 | 0.0397 |
| Fallis | Reward | 24.1 | 0.636 | 0.570 | 0.277 | 0.123 | 0.145 | 0.0269 | 0.0452 |
| | Red Bobs | 26.1 | 0.565 | 0.574 | 0.269 | 0.106 | 0.157 | 0.0260 | 0.0385 |
| Nitrogen basis 100 | | | | | | | | | |
| Edmonton | Reward | | 100 | 35.5 | 18.3 | 12.8 | 10.1 | 1.3 | 4.2 |
| | Red Bobs | | 100 | 52.1 | 48.5 | 14.8 | 12.1 | 1.4 | 4.5 |
| Fallis | Reward | | 100 | 89.6 | 43.6 | 19.3 | 22.8 | 4.2 | 7.1 |
| | Red Bobs | | 100 | 101.5 | 47.6 | 18.8 | 27.8 | 4.6 | 6.8 |

definitely higher in the Edmonton grain while all other constituents were in general higher in the Fallis samples. The difference between varieties was only apparent in the weights of nitrogen which were consistently higher in the Reward samples from both soils.

The outstanding differences in the composition of the various grain samples are shown in the lower section of Table VI, where the weight of each of the other nutrients is compared with nitrogen expressed as 100. Fallis grain had a much higher proportion of ash and ash constituents to nitrogen, than Edmonton grain. Red Bobs had a much higher proportion of total ash, and a slightly higher proportion of potassium and phosphorus, to nitrogen than did Reward.

Percentage Data.

Nitrogen, Ash and Ash Constituents as a Percentage of Dry Matter. Nitrogen ash and ash constituents of the final collection expressed as percentages of the dry matter are shown in Table VII, together with accompanying "t" values which indicate the significance of differences due to soil and variety.

In accord with previous results on the composition of the whole plant, the percentages of nitrogen and all ash constituents except phosphorus were higher in the straw of Edmonton samples. This condition was, however, reversed in the grain where all the constituents, except

TABLE VII

Percentage data for straw and grain of the mature plants and the significance of differences due to soil and variety

| Determination | Part of plant | Mean of 8 replicate samples | | | | "t" values | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Edmonton | | Fallis | | Difference between general levels+ at Edmonton and Fallis | Difference between varieties++ | | Difference between varietal reaction at Edmonton and Fallis |
| | | Reward | Red Bobs | Reward | Red Bobs | | Edmonton | Fallis | |
| Percentage of dry matter | | | | | | | | | |
| Nitrogen | Grain | 3.37 | 2.89 | 2.31 | 1.91 | 22.37** | 50.30** | 43.65** | 6.12** |
| | Straw | 0.62 | 0.59 | 0.37 | 0.32 | 5.92** | 9.82** | 9.88** | 1.13 |
| Ash | Grain | 1.70 | 1.57 | 2.08 | 1.94 | -6.12** | 7.51** | 5.02** | 1.77 |
| | Straw | 7.52 | 6.82 | 7.85 | 6.02 | 1.01 | 4.95** | 10.42** | 3.87** |
| Phosphorus | Grain | 0.61 | 0.53 | 1.01 | 0.91 | -18.90** | 3.47** | 5.09** | 1.38 |
| | Straw | 0.087 | 0.078 | 0.280 | 0.194 | -8.80** | 0.51 | 4.95** | 3.14** |
| Sulphur | Grain | 0.43 | 0.43 | 0.45 | 0.36 | - | - | - | - |
| | Straw | 0.41 | 0.37 | 0.15 | 0.18 | - | - | - | - |
| Potassium | Grain | 0.34 | 0.35 | 0.53 | 0.53 | -15.85** | -0.53 | 0.19 | 0.60 |
| | Straw | 1.01 | 1.05 | 0.86 | 0.71 | 5.17** | -0.06 | 3.84** | 2.76* |
| Calcium | Grain | 0.042 | 0.040 | 0.098 | 0.088 | -4.72** | 1.80 | 1.79 | 0.65 |
| | Straw | 0.30 | 0.28 | 0.21 | 0.17 | 12.07** | 2.31* | 3.08** | 0.55 |
| Magnesium | Grain | 0.140 | 0.131 | 0.165 | 0.130 | -2.44* | 2.76** | 10.45** | 5.44** |
| | Straw | 0.067 | 0.040 | 0.040 | 0.025 | 4.62** | 2.95** | 1.55 | 0.99 |
| Percentage of ash | | | | | | | | | |
| Phosphorus | Grain | 35.5 | 32.9 | 48.5 | 46.8 | -10.89** | 1.73 | 1.34 | 0.65 |
| | Straw | 1.16 | 1.17 | 3.60 | 3.21 | -14.72** | -0.34 | 2.24* | 1.82 |
| Potassium | Grain | 20.0 | 22.5 | 25.6 | 26.8 | -3.65** | -1.53 | -0.76 | 0.55 |
| | Straw | 13.6 | 15.1 | 11.0 | 11.9 | 3.31** | -2.52* | -1.36 | 0.82 |
| Calcium | Grain | 2.48 | 2.43 | 4.69 | 4.57 | -10.12** | 0.29 | 0.61 | 0.22 |
| | Straw | 4.02 | 4.13 | 2.71 | 2.91 | 6.63** | -0.70 | -1.28 | 0.42 |

+ Minus sign indicates a higher percentage in Fallis plants.
++ Minus sign indicates a higher percentage in Red Bobs than Reward.
* 5% point, t = 2.15.
** 1% point, t = 2.98.

nitrogen, were definitely higher in the Fallis samples. Calcium, potassium and phosphorus, in particular, were much higher due to the greater translocation of calcium and potassium to the grain in the Fallis samples (Table V) and the consistently higher amounts of phosphorus at all times present in the Fallis plants.

Varietal differences were definite. The percentage of ash constituents was higher in Reward despite the greater translocation of nutrients to the grain by Red Bobs. The varietal differences were on the whole more definite in the composition of the straw. This was particularly so at Fallis where the percentage of every constituent determined, except magnesium, was significantly higher in Reward samples.

The differences between the varietal reactions at Edmonton and Fallis showed that the percentage of nutrients in Reward was higher on both soils, but that this difference between the varieties was often greater at Fallis. Nitrogen in the grain was exceptional, the difference between the two varieties being significantly higher at Edmonton.

Ash Constituents as a Percentage of Total Ash. Phosphorus, potassium, calcium and magnesium expressed as percentages of the total ash in the final collection are shown in Table VII, together with accompanying "t" values which indicate the significance of the differences due to soil and variety.

In spite of the significant differences in ash expressed as a percentage of dry matter, these results show the same relation between soils as did the previous results expressed on a dry matter basis. The differences between varieties were, however, no longer significant and indicated that the composition of the ash was not altered as much as the composition of the dry matter.

The results show that the soil greatly influenced the composition of the grain and straw of the final collection. The percentage of nutrients translocated to the grain was so much greater at Fallis that the composition of the grain became richer and the composition of the straw poorer than at Edmonton. Phosphorus, however, was higher in both grain and straw of the Fallis samples. Translocation to the grain tends to be so regulated that under very diverse nutritional conditions the composition of the grain will be much more nearly uniform than that of the straw. The composition of the mature straw varied greatly and the effect of soil or variety in altering the composition was much more definite in the straw than in the whole plant.

## Quality of Grain.

The quality of the wheats grown in this experiment was determined by the usual experimental baking procedure. During 1932 and 1933 Reward and Red Bobs were grown under conditions similar to those of this experiment, and in Table VIII the quality of the wheats for the three years is compared by means of protein and loaf volume results.

TABLE VIII

Comparison of quality of Reward and Red Bobs grown at Edmonton and Fallis

| Sample | | Protein, % | | | Loaf volume, cc. | | |
|---|---|---|---|---|---|---|---|
| | | 1932 | 1933 | 1934 | 1932 | 1933 | 1934 |
| Edmonton | Reward | 16.5 | 16.8 | 16.6 | 708 | 795 | 668 |
| | Red Bobs | 14.2 | 14.7 | 14.2 | 632 | 694 | 545 |
| Fallis | Reward | 13.6 | 12.6 | 11.4 | 662 | 627 | 515 |
| | Red Bobs | 10.3 | 10.6 | 9.4 | 588 | 632 | 464 |

The differences in loaf volume results show, as has previously been indicated, that Reward was in general higher in quality than Red Bobs at both Edmonton and Fallis. This original quality of the wheats is very closely related to protein content, and both loaf volume and protein results show that this relationship between the varieties was with one exception the same for all three years. There was, however, a considerable fluctuation in the results from year to year. The 1934 loaf volume results are particularly low in comparison with the 1932 and 1933 results. This can be attributed in part to the climatic conditions of the year, since nearly all wheat grown in central and northern Alberta was of comparatively low quality in 1934, and in part to the effect of a frost on August 22. The frost occurred when the percentage of dry matter in the grain was approximately 58%. Newton and McCalla (14) concluded that when the grain contained 58%

dry matter it had reached a critical stage of development after which little or no translocation of nutrients took place. Thus it is assumed that in this experiment translocation to the grain was not affected, although the baking quality of the flour, as indicated by loaf volume results, may have been slightly lowered.

## Discussion

The results of the chemical analyses of the developing plants have been expressed in a number of different ways in order that as many differences as possible between varietal and soil reactions might be emphasised. It is unfortunate that the individual total weight results were not more accurate but the stands of wheat, particularly at Fallis, were not uniform, and the samples from each sub-block often varied greatly even though the total weights per collection, representing 48 six-inch sections, undoubtedly were fairly accurate. Larger samples could not be used because of the difficulty in handling in the laboratory. The method of sampling would have been improved by collecting a definite number of plants and then determining the comparative yields of the varieties on the two soils by counting the number of plants per unit length of row.

The effect of the soil in altering growth and composition of the developing plants is definite. The general fertility and ability of the black (Edmonton) in comparison with the gray (Fallis) soil to produce a crop is clearly illustrated in the total weight results. This difference in yield was reflected in the composition of the plants, Edmonton samples having a definitely higher amount of all nutrients except phosphorus. This difference in phosphorus is interesting because when expressed as a percentage of dry matter or ash it was significantly higher in Fallis plants at all stages of maturity. Soil analyses show that this high phosphorus was not due to the total amount of this element in the gray soil which is less than that present in the black soil.

Fertilizer experiments (22,39) have shown that nitrogen and sulphur are limiting in the Fallis soil and the results presented in this paper in every case substantiate these findings. The shape of the total weight curves for nitrogen and sulphur, the ratios of equivalent uptake of nitrogen, sulphur and phosphorus, the percentage rate of uptake of nitrogen and sulphur and the low percentage of nitrogen in Fallis samples, all indicate that nitrogen and sulphur were limiting growth at Fallis very early in the development of the plant. In addition it was shown that the anion:cation ratio was approximately the same for plants grown on both soils. It is suggested therefore

that there is a controlling influence which maintains a fairly constant anion:cation ratio under different nutritional conditions, and that when two of the important anions, nitrogen and sulphur, are limiting, the anion: cation ratio will be maintained at approximately the normal level by a greater absorption of phosphorus. In the Fallis plants this greater absorption of phosphorus was at first sufficient to keep the anion:cation ratio as high as in Edmonton plants, but in the later stages of maturity it was apparently not sufficient and the ratio dropped slightly below that in the Edmonton plants.

The effect of soil in altering the composition of the grain and straw of the final collection must be considered separately as it was not the same as on the whole plant. In the growing plant all nutrients except phosphorus were higher as a percentage of dry matter in the Edmonton samples, but in the grain this condition was almost reversed and all the elements except nitrogen were higher in the Fallis samples. The translocation of nutrients to the grain was so much greater in the Fallis plants that the grain became richer and the straw poorer than in the Edmonton plants. The higher proportion of the calcium translocated to the grain in the Fallis plants resulted in a percentage of calcium in the grain twice as high as in the Edmonton plants. Similarly a much greater proportion of the sulphur was translocated to the grain in the Fallis samples, but owing to the limiting supply of this

element the greater translocation only brought the sulphur percentage of the Fallis grain to about the same level as that of the Edmonton grain. It did, however, markedly lower the sulphur content of the Fallis straw.

The percentage rate of uptake of nutrients from the black soil, where there was a relatively abundant supply of all nutrients, rose to a maximum at about the time of heading, while on the gray soil this rate for nitrogen and sulphur was at a maximum before the first collection. This means that at Fallis the limiting elements were most available during the early stages and the growth which was initiated could not be carried through to maturity without a marked alteration in the percentage composition of the plant.

The effect of variety in determining the composition of the wheat plant has generally been observed in its effect on the composition of the mature grain or straw. No systematic study of the effect of variety in controlling the composition of the whole plant at progressive stages of maturity has come to the attention of the author . This study shows that for certain elements expressed as a percentage of dry matter the composition of the two varieties was significantly different at practically all stages of development. Reward was significantly higher than Red Bobs in nitrogen at all collections on the black soil and in total ash, phosphorus and potassium for four collections on the gray soil. At the time of the last collection the

difference between the varieties was more marked, especially in the composition of the straw, than at any other collection.

The ratio of grain to straw and the proportion of nutrients translocated to the grain will determine in a large measure the composition of the grain which in turn will affect the quality of the flour. Varietal differences in this respect were found. Red Bobs, for example, produced, on both soils, a greater proportion of grain to straw than Reward, the difference between the varieties being greater at Fallis. This greater proportionate production of grain by Red Bobs, grown under the less favourable gray soil conditions, was accompanied by a still greater proportionate translocation of nutrients to the grain, but despite this, the grain of Red Bobs was lower in most constituents than that of Reward.

Soil and variety have definitely affected the quality of the wheats produced and also the keeping property of the flour milled from this wheat. An attempt to relate the differences in absorption already noted to these changes in quality is as yet largely a matter of speculation. Nitrogen absorption and the percentage of protein in the grain is undoubtedly the main factor in determining the original quality of the grain, but the varietal differences in the deterioration of the flour must be due to other causes.

Wood (36) as early as 1907 suggested that the

development of the plant might affect the quality of the proteins produced in the grain. He believed that acids and salts in the cell sap during endosperm formation impress upon the gluten the physical properties which decide the character of the flour obtained from that wheat. Gericke (9) extended this idea, and suggested that the plant sap, even before endosperm formation, might influence directly the quality of the proteins. He has, with other workers (5), stressed the particular importance of minerals in this regard. It is interesting to note that in this particular experiment the ratio of minerals to protein was higher at Fallis and higher in Red Bobs than in Reward, but it must be admitted that the relation between nutrition and keeping properties of flour is a different problem from that under discussion by Wood and Gericke.

In the Fallis plants the nitrogen-phosphorus-sulphur balance is very different from that in the Edmonton plants. Since these elements are important constituents of the proteins it is possible that the composition of the Fallis grain was altered in some way which affected quality. If this is the cause the reason for the much more rapid deterioration of Red Bobs flour is not clear.

The importance of lipoidal substances in affecting the physical properties of the wheat proteins is also known (38). Storage experiments (31) with flour from Edmonton and Fallis wheat have shown that there are greater changes in the lipoidal substances in the Fallis flour,

and it seems certain that these changes are related to the deterioration of the baking quality of the flour. Phosphorus is an important constituent of these lipoidal substances, and the greater uptake of phosphorus by plants grown at Fallis may in some way alter the metabolism of these plants so that the particular lipoidal substances formed are more susceptible to alteration than similar substances found in the grain grown at Edmonton.

The studies reported in this part of the paper have not necessarily shown all of the important differences which may exist in the mineral nutrition of wheat grown on the black and gray soils. The importance of other elements needed in smaller amounts has been increasingly recognized in plant nutrition studies, and it seems equally possible that some of these might influence the keeping properties of flour.

## Conclusions

1. Soil and varietal differences definitely influenced the composition of the plants.

2. The weights of dry matter and all nutrients studied were higher for the plants grown at Edmonton.

3. As a percentage of dry matter all nutrients except phosphorus were higher in the Edmonton plants.

4. Reward was higher than Red Bobs in the percentage of nitrogen when grown at Edmonton and ash,

phosphorus and potassium when grown at Fallis.

5. The grain of Fallis plants was higher in all ash constituents but lower in nitrogen.

6. Varietal differences were more definite in the composition of the grain than the whole plant. Reward grown on both soils was significantly higher in the percentage of nitrogen, ash, phosphorus and magnesium in the grain.

7. The data for total weights, percentages, rates of uptake and ion ratios all show that nitrogen and sulphur limited growth at Fallis.

8. It was suggested that the high phosphorus uptake by wheat grown at Fallis was in compensation for the low supply of nitrogen and sulphur.

9. The total anion:cation ratios for plants grown on the two soils are much more nearly alike than are the ratios of individual pairs of ions.

10. The differences in the original quality of the wheat grown on the two soils can be largely accounted for by differences in protein level, and therefore nitrogen supply.

11. The differences in keeping properties of the flour are suggested as being connected with:

(a) Ash:nitrogen relationship in grain which was definitely higher in Fallis plants.

(b) The nitrogen:phosphorus:sulphur balance which was very different for plants grown on the two soils.

(c) Total phosphorus. The high phosphorus in the Fallis plants may affect the phosphatide content of grain. Phosphatides are known to be related to original quality and keeping property of flour.

# PART II

## The Distribution of Phosphorus and Nitrogen, and Various Phosphorus Fractions in the Developing Grain of Reward and Red Bobs Grown at Edmonton and Fallis

### Introduction

The study of the absorption by Reward and Red Bobs grown at Edmonton and Fallis showed that one of the chief differences was the much greater proportionate absorption of phosphorus from the gray soil. This caused a definite increase in the percentage of phosphorus in the vegetative parts of the plant and a slight increase in the percentage of phosphorus in the grain.

It is known that certain phosphorus containing substances such as phosphatides, have a direct influence on wheat quality and keeping properties of flour. It was thought, therefore, that the higher phosphorus in the Fallis grain might in some way be connected with the quality and keeping properties of the flour. It was decided to study the distribution of phosphorus in the developing grain of Reward and Red Bobs grown on the two soils to determine whether the differences in the phosphorus fractions were of the same order as the differences in

total phosphorus.

Many analyses of the developing wheat kernel have been made, and a good review of the subject up to 1925 is given by Bailey (4). The changes in the nitrogen content have been studied in detail by Woodman and Engledow (37) who have shown definitely that total nitrogen as a percentage of dry matter decreases for about 35 days after flowering and then increases until the grain is ripe. Similar but less extensive studies for the distribution of phosphorus were made by Rousseaux and Sirot (28) who showed that the phosphoric acid content tended to parallel that of nitrogen.

Phosphorus is believed to occur in the grain in the following forms:

(1) Phytin
(2) Phospholipoids
(3) Hexose phosphate
(4) Nucleic acid
(5) Phosphoproteins

No practical methods are, however, available for dividing the total phosphorus into these various fractions. Knowles and Watkins (13) studied the distribution of nitrogen and phosphorus in the growing wheat plant and ear. They reported total, lipoid, phytin and inorganic phosphorus and showed that at maturity the total phosphorus in the ear was made up of 49.3% phytin, 2.9% lipoid and 47.8% inorganic phosphorus. Their inorganic phosphorus was obtained by subtracting phytin plus lipoid from total

phosphorus and must have contained phosphorus in the form of nucleic acids and phosphoproteins.

Mather (17) determined the amounts of certain phosphorus fractions in hay. He reports the phosphorus in a 1% hydrochloric acid extract, and the inorganic, total organic, soluble and insoluble organic fractions.

Deturk (7) analysed corn plants for total phosphorus and alcohol soluble, inorganic, soluble organic and acid insoluble fractions. Many other workers have carried out similar investigations with various plants. The methods of analysis reported vary considerably and were in general carried out on the dried material.

In order to present a true picture of the distribution of the various phosphorus fractions in the living plant it was decided to use only fresh material. Michel-Durant (21), in a study of the phosphorus metabolism of the mistletoe plant, described a method for the determination of six phosphorus fractions in the fresh leaf. The methods employed in this experiment were an adaptation of those reported by him.

## Experimental Material

During the summer of 1935 Reward and Red Bobs wheat were grown on adjacent 1/20 acre plots at Edmonton and Fallis under conditions similar to those of the 1934 experiment.

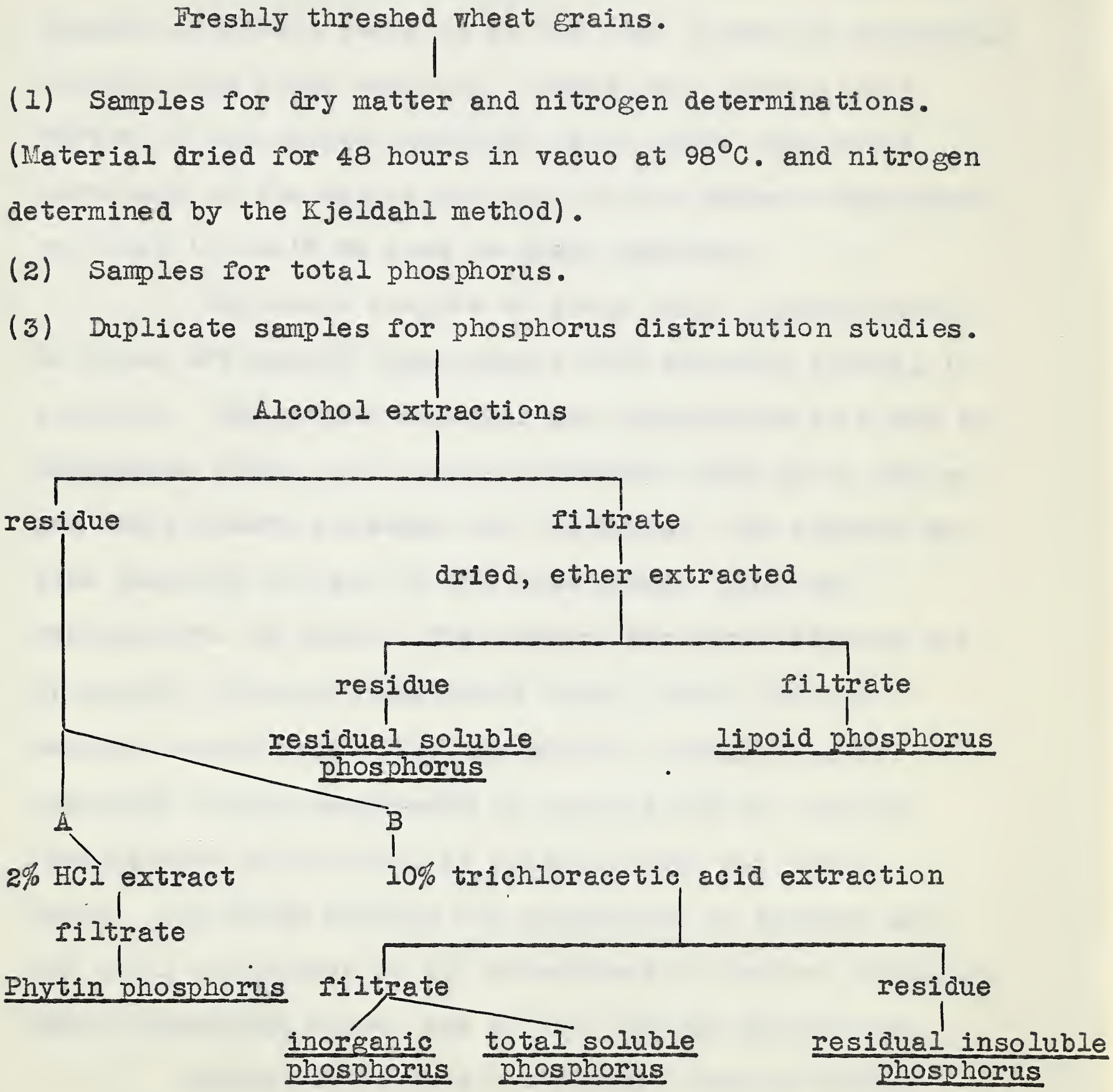
Heads at the same stage of maturity were obtained by tagging the centre culm at the beginning of flowering. Thirty-five hundred heads of each variety were tagged at Edmonton on July 16 and 18 respectively. At Fallis it was estimated that the varieties were one day later in flowering than at Edmonton, and 1500 heads of each variety, at the same stage of development, were tagged on July 19.

Collections of heads of both varieties were made at 8.00 a.m. twice a week at Edmonton and once a week at Fallis. Enough heads to give the required weight of sample were collected at random from the plots and conveyed immediately to the laboratory. The grain was threshed out by hand and used at once for the various chemical determinations.

At Edmonton on the night of August 15 the temperature dropped below the freezing point for at least six hours. The minimum temperature recorded in the wheat field at approximately three feet above ground level was 24°F. This frost occurred when the kernels of Reward and Red Bobs contained 43.6% and 41.3% dry matter and stopped translocation of nitrogen to the kernels. Small sections of the plots were, however, protected by fires. The grain in these areas was very little damaged, as determined by weight of 1000 kernels, and was used for the last four collections. A frost also occurred at Fallis, and although it was not nearly as severe it probably had some effect on translocation.

## Methods of Analysis

Scheme of Analysis.



(1) Samples for dry matter and nitrogen determinations. (Material dried for 48 hours in vacuo at 98°C. and nitrogen determined by the Kjeldahl method).

(2) Samples for total phosphorus.

(3) Duplicate samples for phosphorus distribution studies.

Total Phosphorus: - The fresh grain was digested in a Kjeldahl flask using nitric and sulphuric acids. Phosphorus was precipitated as ammonium phosphomolybdate

and determined by titration with standard sodium hydroxide solution. The details of the method are described by Richards and Godden (27).

Lipoidal Phosphorus: - There has been much discussion of recent years as to the best method of extracting lipoids from plant material. Sando (29) gives a good review of the methods employed up to 1928. The chief advantage of the method employed in the present experiment was that it could be used on fresh material.

Duplicate samples of fresh grain (approximately 10 grams dry weight) were ground with absolute alcohol in a mortar. The ground material was transferred to a 200 cc. Erlenmeyer flask, the volume of alcohol made up to 100 cc. and the contents refluxed for two hours. The alcohol was then decanted off and 75 cc. more added. This was refluxed for 12 hours. The alcohol was then filtered off by suction through a sintered glass funnel and the residue washed once. The two alcohol extracts were combined, slowly evaporated to dryness and the residue re-extracted with 75 cc. of boiling ether for three hours. The ether extract was evaporated to dryness and the total phosphorus in it, determined by the wet digestion method described above, was called "lipoid phosphorus".

Sando states that the alcohol extract simultaneously removes with the lipoids most of the soluble carbohydrates which interfere with the subsequent extraction of the syrupy residue with ether. Digestion of the

ether extract by nitric and sulphuric acids was a very slow process. It was often more than 15 hours before a clear colourless solution was obtained.

Residual Soluble Phosphorus: - Total phosphorus in the residue from the ether extract, determined by wet digestion method, was called "residual soluble phosphorus". This fraction varies with the amount of water in the fresh material and the consequent dilution of the alcohol and probably contained much inorganic phosphorus in the earlier collections.

Inorganic Phosphorus: - The residue from one of the duplicate alcohol extracts was re-extracted with 200 cc. of 10% trichloracetic acid for three hours with continual shaking. Aliquots of the filtrate were used for the determination of total soluble and inorganic phosphorus. The latter fraction was precipitated as strychnine molybdophosphate, dried at 110°C. and then weighed. The method was an adaptation of the Embden-Fetter gravimetric method for inorganic phosphate of serum, plasma or blood as described by Peters and Van Slyke (24).

The method was very satisfactory if the amount of $P_2O_5$ in the aliquot was reduced to one mgm. If the precipitate was any larger it was very difficult to filter, and due to its flocculent nature it probably carried down other phosphorus containing substances besides the inorganic forms.

Total Soluble Phosphorus: - This fraction was determined on an aliquot of the trichloracetic acid extract and probably includes the phytin and inorganic fractions.

Residual Insoluble Phosphorus: - This fraction included all the phosphorus in the residue from the trichloracetic acid extract. It represents mainly the phosphorus in the form of phosphoproteins and nucleic acids.

Phytin Phosphorus: - The residue from the second duplicate alcohol extract was re-extracted for three hours with 200 cc. of 2% hydrochloric acid with continual shaking. Aliquots of the filtrate were titrated with ferric chloride using 1 cc. of 5% sodium salicylate as an indicator. The method was Averill and King's (3) modification of the original Heubner and Stadler method.

The drawback to this method was the formation of a slow settling flocculent precipitate which obscured the end point. More accurate methods have been devised. Andrews and Bailey (2) suggested titrating short of the end point and then completing the titration on the filtrate. Harris and Mosher (10) suggested titrating beyond the end point, filtering and determining the amount of excess ferric chloride in the solution by comparison of the colour with a solution of known strength. These methods are more laborious and for the purpose of the present experiment the method used was considered sufficiently accurate. Phosphorus in all the fractions was reported as $P_2O_5$.

It cannot be claimed that the above scheme for the fractionation of the total phosphorus is wholly satisfactory or even that the fractions represent definite types of phosphorus compounds. The methods adopted are, however, relatively simple in their procedure and are practicable from the point of view of time and labour involved in their carrying out. They enable the total phosphorus of the grain to be partitioned at every stage of development into a series of comparable fractions and thus make possible the comparison, in a broad sense, of the phosphorus metabolism of grain when grown on the black and gray soils.

## Results

### Total Nitrogen and Phosphorus.

The results for total nitrogen and phosphorus in the grain at progressive stages of maturity are shown graphically in Fig. 10. The top two curves represent nitrogen and phosphorus as a percentage of dry matter, and the two lower curves as total weights per 1000 kernels.

Nitrogen as a percentage of dry matter decreased for approximately 25 days after flowering and then increased. These results are in agreement with other work of this nature. In the early stages of the development of the grain the percentage of nitrogen decreased because

endosperm was being formed which was lower in nitrogen content than the bran layers. Later in development, when the majority of the endosperm had been formed, the percentage of nitrogen increased due to the loss of carbohydrates by respiration. The changes in phosphorus as a percentage of dry matter ~~are~~ were very similar to the changes in nitrogen. The shape of the curves for the two constituents were much the same except that the minimum point on the phosphorus curves was reached a few days later than it was for nitrogen.

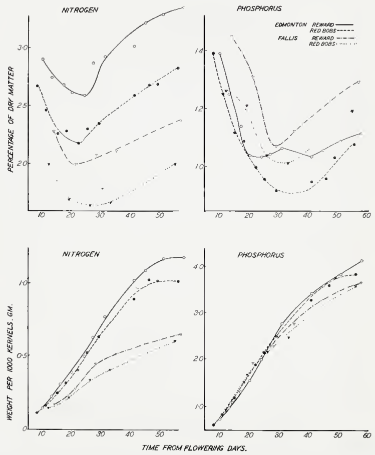


Fig. 10. Total nitrogen and phosphorus in the developing grain of Reward, Red Bobs, grown at Edmonton and Fallis.

Nitrogen was at all times definitely higher in Reward than in Red Bobs and also in Edmonton as compared with Fallis grain. The differences between varieties and soils in the percentage of phosphorus were also quite

definite. Reward was consistently higher than Red Bobs but, as had been shown in previous analyses, the percentage of phosphorus was higher in the Fallis grain.

The total weights of nitrogen and phosphorus in 1000 kernels gradually rose to a maximum at about the fiftieth day after flowering for nitrogen and a few days later for phosphorus. The weights of phosphorus in grain from both soils were approximately the same until about the twenty-fifth day after flowering when the phosphorus in the Fallis grain fell slightly below that in the Edmonton grain.

The rate of translocation to the grain of nitrogen and phosphorus is shown in Table IX for Red Bobs grown at Edmonton and Fallis. The rate, which rises to a maximum and then falls, is represented by the increase in weight of the constituents in 1000 kernels per day. The translocation of nitrogen did not altogether follow the translocation of phosphorus. The ratios in the last column of the table compare the rate of translocation of nitrogen and phosphorus. Phosphorus was translocated comparatively faster in the earlier stages of the development of the grain and reached its maximum rate of translocation a week or so before nitrogen translocation reached a similar maximum.

TABLE IX

The translocation of nitrogen and phosphorus
to the grain and the ratio
of nitrogen:phosphorus

| Sample | Days from flowering | Gain per day, mgm. | | Ratio nitrogen: phosphorus |
|---|---|---|---|---|
| | | Nitrogen | Phosphorus | |
| Red Bobs | | | | |
| Edmonton | 0-11 | 14.8 | 7.57 | 1.96 |
| | 11-18 | 20.6 | 9.66 | 2.13 |
| | 18-25 | 29.3 | 9.30 | 3.15 |
| | 25-29 | 28.3 | 4.69 | 6.03 |
| | 29-41 | 21.5 | 6.58 | 3.27 |
| | 41-56 | 8.2 | 3.81 | 2.15 |
| Red Bobs | | | | |
| Fallis | 0-12 | 12.2 | 7.83 | 1.56 |
| | 12-19 | 10.3 | 10.71 | 0.96 |
| | 19-26 | 17.3 | 6.57 | 2.63 |
| | 26-33 | 23.5 | 4.43 | 5.30 |
| | 33-35 | 9.0 | 5.15 | 1.75 |

## Phosphorus Fractions as a Percentage of Dry Matter and Total Phosphorus.

The results for the six phosphorus fractions expressed as a percentage of dry matter are presented in Table X for Red Bobs grown at Edmonton and Red Bobs and Reward grown at Fallis. The total soluble, inorganic, residual insoluble and lipoid fractions for Edmonton and Fallis Red Bobs are represented graphically in Fig. 11.

Phytin phosphorus is the chief storage form of phosphorus in the grain, and the results show that as the grain matured it gradually increased as a percentage of

TABLE X

Total phosphorus and phosphorus fractions as a percentage of dry matter

| Soil | Sample | Days from flowering | % dry matter | Total phosphorus | Phosphorus fractions as percentage of dry matter | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Phytin | Total soluble | In-organic | Residual in-soluble | Lipoid | Residual soluble |
| Edmonton | Red Bobs | 8 | 25.2 | 1.39 | 0.151 | - | 0.420 | - | - | 0.046 |
| | | 11 | 26.8 | 1.25 | - | 0.604 | 0.388 | 0.365 | 0.151 | 0.089 |
| | | 15 | 29.9 | 1.12 | 0.348 | 0.532 | 0.339 | 0.259 | 0.135 | 0.118 |
| | | 18 | 35.0 | 1.09 | 0.410 | 0.540 | 0.260 | 0.207 | 0.108 | 0.169 |
| | | 22 | 39.3 | 1.00 | 0.401 | 0.584 | 0.225 | 0.242 | 0.109 | 0.069 |
| | | 25 | 43.2 | 0.96 | 0.383 | 0.544 | 0.164 | 0.216 | 0.098 | 0.027 |
| | | 29 | 46.9 | 0.92 | 0.362 | 0.600 | 0.197 | 0.192 | - | 0.082 |
| | | 41 | 52.5 | 0.95 | 0.366 | 0.644 | 0.209 | 0.107 | 0.074 | 0.017 |
| | | 46 | 56.1 | 0.96 | 0.533 | 0.680 | 0.175 | 0.089 | 0.071 | 0.009 |
| | | 49 | 58.8 | 1.08 | 0.559 | 0.712 | 0.152 | 0.109 | 0.054 | 0.006 |
| Fallis | Red Bobs | 12 | 27.2 | 1.26 | 0.246 | 0.816 | 0.578 | 0.189 | 0.196 | 0.134 |
| | | 19 | 33.2 | 1.21 | 0.371 | 0.624 | 0.315 | 0.168 | 0.130 | 0.110 |
| | | 26 | 41.2 | 1.04 | 0.654 | 0.612 | 0.235 | 0.156 | 0.099 | 0.037 |
| | | 33 | 47.4 | 1.01 | 0.564 | 0.648 | 0.258 | 0.170 | 0.078 | 0.016 |
| | | 55 | 59.8 | 1.19 | 0.492 | 0.844 | 0.178 | 0.094 | 0.060 | 0.000 |
| Fallis | Reward | 14 | 28.6 | 1.45 | 0.262 | 0.828 | 0.587 | 0.193 | 0.194 | 0.183 |
| | | 21 | 35.5 | 1.31 | 0.475 | 0.748 | 0.343 | 0.180 | 0.136 | 0.110 |
| | | 28 | 43.6 | 1.07 | 0.519 | 0.628 | 0.193 | 0.234 | 0.107 | 0.050 |
| | | 35 | 49.6 | 1.13 | 0.452 | 0.776 | 0.202 | 0.166 | 0.079 | 0.016 |
| | | 57 | 61.4 | 1.29 | - | 0.764 | 0.158 | 0.105 | 0.061 | 0.000 |

dry matter. In the Fallis grain there was a slight decrease in the later stages of development, but the maximum percentage was higher than in the Edmonton grain.

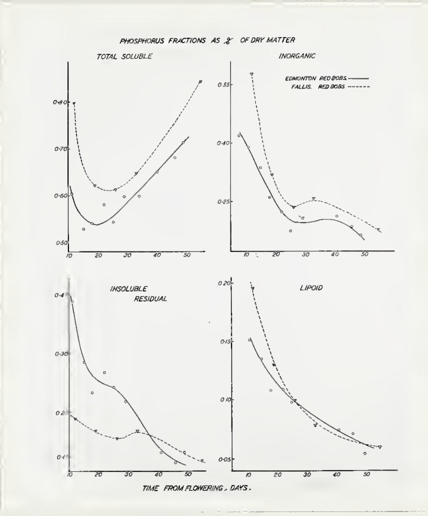


Fig. 11. The percentage of four phosphorus fractions in the developing grain of Red Bobs grown at Edmonton and Fallis.

Total soluble phosphorus was the largest fraction and must have included the phytin and inorganic forms. As a percentage of dry matter it decreased for about 20 days after flowering and then rose, the changes being similar to those for total phosphorus (Fig. 10). The percentage in the Fallis Red Bobs grain was at all times higher than in similar samples from Edmonton.

The percentage of inorganic phosphorus gradually decreased as the grain matured. This is the main form in which phosphorus is translocated in the plant, and the

percentage in the grain depends upon the amount translocated and the proportion converted into other types of phosphorus. The percentage was at all times higher in the Fallis grain.

Residual insoluble phosphorus, which represents phosphorus in the form of nucleic acids and phosphoproteins, was the only fraction that was definitely higher in the Edmonton grain. Twelve days after flowering the percentage in the Edmonton grain was twice as high as that in the Fallis grain, but it fell so rapidly that at maturity there was no appreciable difference in the percentages in the grain from the two soils.

The graphs illustrate the steady fall in the percentage of lipoid phosphorus. There was no definite difference between Edmonton and Fallis grain.

Residual soluble phosphorus varied with the amount of water in the fresh samples and therefore as a percentage of dry matter it gradually decreased as the grain matured.

The results can also be considered in another way by expressing them as a percentage of the total phosphorus (Table XI). The phytin and total soluble fractions were the only fractions that increased as the grain matured. The slight increase in the total soluble fraction was undoubtedly due to its phytin content. Inorganic and lipoid phosphorus decreased regularly while the residual insoluble fraction remained fairly constant until about 30 days after flowering when there was a definite decrease.

Comparing the grain from Edmonton and Fallis the main difference was in the residual insoluble phosphorus which was a higher percentage of the total in the Edmonton grain.

TABLE XI

Phosphorus fractions as a percentage of total phosphorus

| Sample | Days from flowering | Phosphorus fractions | | | | |
|---|---|---|---|---|---|---|
| | | Phytin | Total soluble | In-organic | Residual insoluble | Lipoid |
| Edmonton | | | | | | |
| Red Bobs | 8 | 10.9 | -- | 30.2 | -- | -- |
| | 11 | -- | 48.3 | 31.0 | 29.2 | 12.1 |
| | 15 | 31.1 | 47.5 | 30.3 | 23.1 | 12.1 |
| | 18 | 37.6 | 49.5 | 23.9 | 19.0 | 9.9 |
| | 22 | 40.1 | 58.4 | 22.5 | 24.2 | 10.9 |
| | 25 | 39.9 | 56.7 | 17.1 | 22.5 | 10.2 |
| | 29 | 39.4 | 65.2 | 21.4 | 20.9 | -- |
| | 41 | 38.5 | 67.8 | 22.0 | 11.3 | 7.8 |
| | 46 | 55.4 | 70.5 | 18.2 | 9.3 | 7.4 |
| | 49 | 51.7 | 65.9 | 14.1 | 10.1 | 5.0 |
| Fallis | | | | | | |
| Red Bobs | 12 | 19.5 | 64.8 | 45.9 | 15.0 | 15.6 |
| | 19 | 30.6 | 51.6 | 26.0 | 13.9 | 10.7 |
| | 26 | 62.8 | 58.8 | 22.6 | 15.0 | 9.5 |
| | 33 | 55.9 | 64.2 | 25.5 | 16.8 | 7.7 |
| | 55 | 41.3 | 70.9 | 15.0 | 7.9 | 5.0 |
| Fallis | | | | | | |
| Reward | 14 | 18.1 | 57.1 | 40.5 | 13.3 | 13.4 |
| | 21 | 36.2 | 57.1 | 26.2 | 13.7 | 10.4 |
| | 28 | 48.5 | 58.7 | 18.0 | 21.9 | 10.0 |
| | 35 | 40.1 | 68.6 | 17.9 | 14.7 | 7.0 |
| | 57 | -- | 59.2 | 12.2 | 8.1 | 4.7 |

## Weights of Phosphorus Fractions in 1000 Kernels.

The weights, at progressive stages of maturity, of the six phosphorus fractions in Red Bobs grain grown at

Edmonton and Fallis are shown in Table XII and the weights of the total soluble, inorganic, residual insoluble and lipoid fractions are represented graphically in Fig. 12.

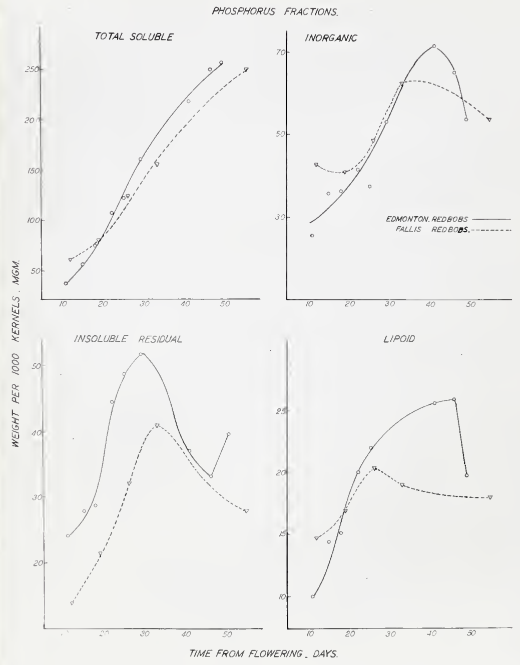


Fig. 12. The total weights of four phosphorus fractions in the developing grain of Red Bobs grown at Edmonton and Fallis.

The phytin and total soluble fractions increased steadily. The shape of the curve for total soluble phosphorus resembled that for total phosphorus (Fig. 10).

TABLE XII

Weight of phosphorus ($P_2O_5$) and phosphorus fractions in 1000 kernels at progressive stages of maturity

| Sample | Days from flowering | Dry weight per 1000 kernels | Total phosphorus | Phosphorus fractions, mgm. | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Phytin | Total soluble | Inorganic | Residual insoluble | Lipoid | Residual soluble |
| | | gm. | mgm. | | | | | | |
| **Edmonton** | | | | | | | | | |
| Red Bobs | 8 | 4.42 | 61.4 | -- | -- | -- | -- | -- | 2.0 |
| | 11 | 6.64 | 83.3 | -- | 40.1 | 25.8 | 24.2 | 10.0 | 7.0 |
| | 15 | 10.64 | 119.3 | 36.9 | 56.6 | 36.0 | 27.6 | 14.3 | 11.7 |
| | 18 | 13.86 | 150.9 | 56.8 | 74.8 | 36.1 | 28.6 | 15.0 | 25.6 |
| | 22 | 18.51 | 185.1 | 53.6 | 108.1 | 41.6 | 44.8 | 20.0 | 12.8 |
| | 25 | 22.59 | 216.0 | 86.5 | 122.9 | 37.1 | 48.8 | 22.3 | 6.4 |
| | 29 | 27.01 | 248.8 | 97.4 | 162.1 | 53.2 | 51.9 | -- | 19.6 |
| | 41 | 34.49 | 327.8 | 126.4 | 220.7 | 71.9 | 36.9 | 25.6 | 4.9 |
| | 46 | 37.25 | 359.2 | 199.0 | 253.3 | 65.1 | 33.2 | 26.3 | 3.7 |
| | 49 | 36.75 | 386.0 | 205.2 | 261.7 | 53.7 | 40.1 | 19.8 | 4.0 |
| **Fallis** | | | | | | | | | |
| Red Bobs | 12 | 7.43 | 94.0 | 18.2 | 60.6 | 42.9 | 14.0 | 14.6 | 10.0 |
| | 19 | 12.98 | 169.0 | 48.2 | 81.1 | 40.9 | 21.8 | 16.9 | 14.2 |
| | 26 | 20.60 | 215.0 | 134.7 | 126.1 | 48.4 | 32.1 | 20.4 | 7.6 |
| | 33 | 24.27 | 246.0 | 136.8 | 157.3 | 62.6 | 41.3 | 18.9 | 3.9 |
| | 55 | 30.20 | 359.4 | 148.4 | 254.9 | 53.8 | 28.4 | 18.0 | trace |
| **Fallis** | | | | | | | | | |
| Reward | 14 | 7.66 | 111.0 | 19.9 | 63.4 | 45.0 | 14.8 | 14.9 | 14.0 |
| | 21 | 13.63 | 192.0 | 64.7 | 102.0 | 46.8 | 24.5 | 18.5 | 15.3 |
| | 28 | 21.23 | 229.0 | 110.4 | 133.3 | 40.9 | 49.7 | 22.7 | 10.6 |
| | 35 | 24.45 | 276.0 | 110.4 | 189.7 | 49.3 | 40.6 | 19.3 | 3.3 |
| | 57 | 28.31 | 365.2 | -- | 216.3 | 44.6 | 29.7 | 17.3 | trace |

The weights of all other fractions rose to a maximum and then decreased. This suggests that the phosphorus compounds represented by these fractions were broken down during the maturation processes of the grain and the phosphorus stored as phytin phosphorus.

The marked decrease in the weight of residual insoluble phosphorus took place about 35 days after flowering. Woodman and Engledow (37) and Newton and McCalla (23) have shown that a coherent gluten can only be obtained from the grain after desiccation has started or when the grain contains about 55% dry matter, (in this experiment about 45 days after flowering). Undoubtedly the first changes in the proteins or other compounds which are to form gluten must take place several days before this. From the results of this experiment it appears that the proteins which are present prior to the formation of gluten are richer in phosphorus, and that when gluten formation begins a part of this phosphorus is split off and converted into some other form, possibly phytin.

Owing to the larger size of the Edmonton Red Bobs kernels the weight of all fractions, except inorganic in the earlier stages of growth, was higher in the Edmonton samples.

## Phosphorus Fractions in Relation to Protein Nitrogen.

If any of the phosphorus fractions are important in affecting wheat quality or the physical properties of

the proteins their relation to the amount of protein nitrogen occurring in the grain should be of interest. This relation is shown in Table XIII as the weight of the phosphorus fractions expressed as a percentage of the protein nitrogen. The percentage of residual insoluble phosphorus decreased as the grain matured and was approximately the same for grain grown on both soils. This was an indication that the proteins of the grain were richer in phosphorus during the earlier stages of the grain's development, and that the percentage of phosphorus in the proteins was the same for Red Bobs grain grown at both Edmonton and Fallis.

TABLE XIII

Phosphorus fractions as a percentage of protein nitrogen

| Sample | Days from flowering | Phosphorus fractions | | | | |
|---|---|---|---|---|---|---|
| | | Phytin | Total soluble | In-organic | Residual insoluble | Lipoid |
| Edmonton | | | | | | |
| Red Bobs | 11 | -- | 38.1 | 24.5 | 23.0 | 9.5 |
| | 15 | 21.3 | 32.7 | 20.9 | 16.0 | 8.3 |
| | 18 | 21.8 | 29.4 | 13.9 | 11.0 | 5.0 |
| | 22 | 16.2 | 32.7 | 12.6 | 13.5 | 6.1 |
| | 25 | 20.0 | 28.3 | 8.5 | 11.2 | 5.2 |
| | 29 | 17.6 | 29.3 | 9.7 | 9.4 | - |
| | 41 | 15.6 | 27.1 | 8.9 | 4.5 | 3.2 |
| | 46 | 20.8 | 26.5 | 6.8 | 3.6 | 2.7 |
| | 49 | 21.8 | 27.7 | 5.7 | 4.2 | 2.0 |
| Fallis | | | | | | |
| Red Bobs | 12 | 19.6 | 65.2 | 46.3 | 15.0 | 15.7 |
| | 19 | 29.1 | 48.9 | 24.7 | 13.2 | 10.2 |
| | 26 | 47.3 | 44.3 | 16.9 | 11.2 | 7.2 |
| | 33 | 40.5 | 46.5 | 18.6 | 12.2 | 5.6 |
| | 55 | 26.7 | 45.8 | 9.7 | 5.1 | 3.3 |

Lipoid phosphorus which has been suggested as being important in influencing wheat quality was slightly higher in relation to protein nitrogen in the Fallis grain and decreased with the maturity of the grain. Phytin and total soluble phosphorus bore a fairly constant relation to the protein nitrogen, but the percentage was very much higher in the Fallis grain. These results are in agreement with the conclusion of Knowles and Watkins (13) who suggested a relation between protein nitrogen and phytin phosphorus.

## The Effect of Frost on the Proportions of the Phosphorus Fractions.

The frost which occurred when the Edmonton Red Bobs grain contained 46.9% dry matter almost completely stopped the translocation of nitrogen and phosphorus to the grain. It also had a definite effect on certain of the phosphorus fractions. Although this effect of frost is of no apparent importance to the general problem, it seemed advisable to report the observations.

The weight of lipoid phosphorus in 1000 kernels had decreased by 50% eight hours after the frost had ceased. This change was the same in both varieties studied at Edmonton. The following weights of lipoid phosphorus in frozen and unfrozen Red Bobs grain grown at Edmonton illustrate the magnitude of the changes.

Weight of lipoid phosphorus, gm. per 1000 kernels

| Days from flowering | 22 | 25 | 29 | 32 | 36 | 41 | 46 |
|---|---|---|---|---|---|---|---|
| Frozen | -- | -- | 11.5 | 6.8 | -- | -- | -- |
| Unfrozen | 20.3 | 22.3 | -- | - | 25.6 | 25.6 | 26.3 |

Because the weight of all fractions was increasing and because lipoid at this stage of development was only approximately 10% of the total phosphorus, it was not possible to tell definitely into which form of phosphorus the lipoid phosphorus was converted. The sudden increase in the weight of total soluble phosphorus in the collection after the frost was greater than the corresponding increase in total phosphorus, and indicated that the lipoid was converted into this form.

In the sample collected four days after the frost there was also a definite decrease in the weight of phytin phosphorus.

## Conclusions

1. As a percentage of dry matter total phosphorus in the developing grain decreases and then increases in a manner similar to total nitrogen.

2. The percentages of phytin, total soluble and inorganic phosphorus fractions were definitely higher in Fallis grain.

3. The percentage of residual insoluble phosphorus was higher in the Edmonton grain in the earlier stages of development.

4. Calculations of the relation between the phosphorus fractions and protein nitrogen showed that the proportion of phytin and total soluble phosphorus was much higher in the Fallis grain and indicated that the phosphorus composition of the proteins was the same for grain grown on both soils.

5. The higher total phosphorus in the Fallis grain was due mainly to the phosphorus represented by the total soluble fraction, probably phytin and inorganic.

6. Frost caused a very sudden decrease in the amount of lipoid phosphorus, and a slower decrease in the amount of phytin phosphorus.

# PART III

## A Study of the Relationship Between Nitrate and Phosphate Absorption, Using Reward, Red Bobs and Marquis Grown in Nutrient Culture Solutions

### Introduction

In Part I it was suggested that the proportionately greater absorption of phosphorus from the gray soil and its higher concentration in the above ground parts of the gray soil plants was perhaps due to the low availability of nitrogen and sulphur.

The results discussed in this section deal with a preliminary study, made by the use of nutrient culture solutions, on the relationship between nitrate and phosphate absorption.

The severe limitation of any important element from the nutrient culture will cause the plants grown in that culture to be reduced in yield and the absorption of all other nutrients to be decreased. Thomas (22), studying the absorption, utilization and recovery of nitrogen, phosphorus and potassium by apple trees, has emphasized this law of the minimum; he says:

> "The omission of any one of these elements from the complete fertilizer is followed by a decreased absorption of the remaining elements. This decreased absorption resulting in a nutritional lack of balance as exhibited in reduced growth and flowering."

Limitations of elements at later stages in the growth period of plants have, however, caused an increase in the absorption of certain of the other elements, and the results reported in this experiment show that a limitation of nitrogen throughout the growth of the plant caused an increase in the total absorption of phosphorus as compared with the complete culture. The type of results obtained depends, of course, on the degree of limitation.

Even though the total absorption of the non-limiting elements may be decreased and the total yield of the plant lowered, as a percentage of the dry matter certain of the non-limiting elements are often increased. This has been shown to be the relationship between nitrogen and phosphorus. Hoagland (11) states

> "In our experiments on wheat we found that omitting the phosphate in the later stages of growth produced a very large increase in the nitrogen content of the grain."

On the other hand a high concentration of phosphorus in the soil will cause a decrease in the percentage of nitrogen in the plant. Krügel et al (15), working with barley in pot cultures showed that the nitrogen in the grain was definitely decreased by phosphorus fertilization.

Similarly, an alteration in the nitrogen supply will cause a change in the percentage of phosphorus in the plant. Proebsting (25) with orchard trees and Kraybill (14) with the tomato have shown that nitrogen fertilizers will increase the percentage of nitrogen in the plant but decrease the percentage of phosphorus.

It seems to be fairly well established, therefore, that a high or low availability of phosphorus will decrease or increase the percentage of nitrogen in the plant, and that a high availability of nitrogen will decrease the percentage of phosphorus in the plant.

The studies reported here deal particularly with the one phase of the nitrogen-phosphorus relationship for which no results are apparently available, and the phase which is of particular interest in regard to nutritional conditions in Fallis soil; the effect of limiting nitrogen supply on the percentage of phosphorus in the plant.

## Experimental Material

Three series of material were produced in the course of this experiment. The first and most complete series consisted of four lots of Marquis wheat each grown in tanks measuring 30 x 60 x 8 inches. The plants were germinated on cheesecloth over a nutrient solution

and transferred to the tanks when one week old. Each plant was set in an individual cork, and there were 128 plants to each culture tank. The solutions in the tanks were aerated for half an hour daily, the air being introduced through perforated rubber tubing laid at six inch intervals over the whole bottom of the tank. Pressure was supplied by an air compressor operating at approximately five pounds per square inch. This maintained a constant and uniform air flow which did not harm the roots. Each of the other two series consisted of three tanks 30 x 30 x 8 inches with 64 plants in each. Reward was grown in one series and Red Bobs in the other. The seeds were germinated and the plants treated in the same manner as in the first series, except that no aeration was used.

The solutions used in the various tanks are recorded in Table XIV and their chemical composition in Table XV. It was necessary to add the nitrogen or phosphorus salts to the limited cultures at short intervals or else for a considerable part of the time the plants would have been growing in solutions free of these nutrients. It was therefore decided to use solutions one-quarter the strength of the usual Hoagland solution, and to renew them in all tanks every 10 days instead of every month as Hoagland suggests. The small amounts of nitrate in cultures 2 and 3 and phosphate in culture 4 were added every two days.

## TABLE XIV

Solutions supplied to various cultures

| Culture No. | Variety | First month | Remainder of development | Abbreviated description |
|---|---|---|---|---|
| 1 | Reward<br>Red Bobs<br>Marquis | Complete | Complete | Complete |
| 2 | Reward<br>Red Bobs<br>Marquis | Complete | Low nitrogen x $\frac{1}{2}$ | Complete: low nitrogen |
| 3 | Reward<br>Red Bobs<br>Marquis | Low nitrogen | Low nitrogen | Low nitrogen |
| 4 | Marquis | Low phosphorus | Low phosphorus | Low phosphorus |

## TABLE XV

Chemical composition of solutions expressed as cc. of molar solution per litre

| Solution | $KNO_3$ | $Ca(NO_3)_2$ | $KH_2PO_4$ | $Ca(H_2PO_4)_2$ | $MgSO_4$ |
|---|---|---|---|---|---|
| Complete | 1.25 | 1.25 | 0.25 | -- | 0.5 |
| Low nitrogen x $\frac{1}{2}$ | -- | 0.10 | 1.5 | 1.15 | 0.5 |
| Low nitrogen | -- | 0.20 | 1.5 | 1.05 | 0.5 |
| Low phosphorus | 1.5 | 1.25 | 0.0125 | -- | 0.5 |

By using the nitrates and phosphates of both calcium and potassium it was possible to vary the nitrogen and phosphorus content of the cultures without altering the concentration of calcium and potassium.

Iron was added as ferric tartrate (0.5%) at the rate of 1 cc. per litre of solution every third day for the first month and then every second day until vegetative growth ceased.

Samples of each culture were collected at six different stages of the plant's development as shown below.

The time of collection and number of plants per collection

| Variety | Days from seeding | | | | | |
|---|---|---|---|---|---|---|
| | Collection 1 | Collection 2 | Collection 3 | Collection 4 | Collection 5 | Collection 6 |
| Reward | 30 (10)* | 44 (8) | 53 (8) | 66 (8) | 82 (8) | maturity |
| Red Bobs | 30 (5) | 44 (4) | 53 (4) | 66 (4) | 79 (4) | maturity |
| Marquis | 30 (5) | 44 (4) | 53 (4) | 60 (4) | 79 (4) | maturity |

* Figures in brackets represent number of plants in each collection.

## Methods of Analysis

In all collections of the tops and roots were analysed separately. In Collections 5 and 6 the grain and straw were also analysed separately. The methods of analysis were the same as those used in the studies reported in the first part of this paper.

## Results

### General Development of Plants.

Extensive notes were kept of the general vigor and development of the plants in the various cultures. The detailed data are much too bulky to present, but a brief summary is given in Table XVI.

TABLE XVI

General development of plants

| Culture | Yield per plant, gm. | | Average root to top ratio | Average No. | | Growth period, days |
|---|---|---|---|---|---|---|
| | Tops | Roots | | Tillers | Leaves | |
| **Reward** | | | | | | |
| Complete 1 | 5.91 | 0.29 | 0.11 | 6.3 | 23.3 | 95 |
| Complete: low N 2 | 5.35 | 0.42 | 0.14 | 4.5 | 18.7 | 98 |
| Low N 3 | 4.21 | 0.39 | 0.15 | 3.1 | 13.4 | 96 |
| **Red Bobs** | | | | | | |
| Complete 1 | 8.43 | 0.37 | 0.10 | 5.7 | 25.1 | 103 |
| Complete: low N 2 | 6.51 | 0.50 | 0.14 | 3.3 | 18.4 | 99 |
| Low N 3 | 3.78 | 0.34 | 0.15 | 2.2 | 12.2 | 99 |
| **Marquis** | | | | | | |
| Complete 1 | 7.05 | 0.48 | 0.16 | 4.8 | 23.3 | 109 |
| Complete: low N 2 | 5.57 | 0.94 | 0.20 | 3.2 | 17.5 | 103 |
| Low N 3 | 4.32 | 0.84 | 0.24 | 3.1 | 14.0 | 100 |
| Low P 4 | 2.91 | 0.30 | 0.26 | 2.0 | 11.0 | 98 |

The complete culture plants made much better growth, as indicated by total yield and the average number of tillers and leaves, than the plants from any of the

other cultures. Measurements showed that growth in the low phosphorus culture was the poorest and that plants grown in the low nitrogen cultures were less vigorous than those grown in the complete:low nitrogen culture. The increasing order of severity of the treatments was complete, complete:low nitrogen, low nitrogen, low phosphorus.

Root growth was greater in the aerated Marquis cultures. The average root-top ratio was highest in the low phosphorus cultures and definitely higher in the low nitrogen than in the complete cultures.

The deficient culture plants matured earlier than the control plants. The complete culture plants of Reward matured prematurely due to an abnormal condition of the roots, which developed soon after heading, and caused them to blacken and decay. The results for this culture after Collection 4 are, therefore, not comparable to the other complete culture plants.

## Chemical Analyses.

The results for the weights per plant of dry matter, nitrogen, ash, phosphorus, potassium and calcium in the tops and roots of Marquis are shown in Fig. 13 and 14, respectively. The results for Marquis only are presented, as they were representative of the results for Reward and Red Bobs.

# Total weights of nutrients per plant of Marquis at progressive stages of maturity and grown in five different culture solutions

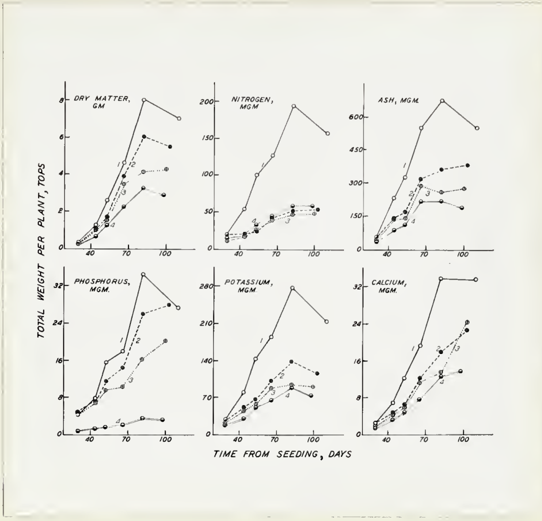


Fig. 13. Total weight in vegetative parts.

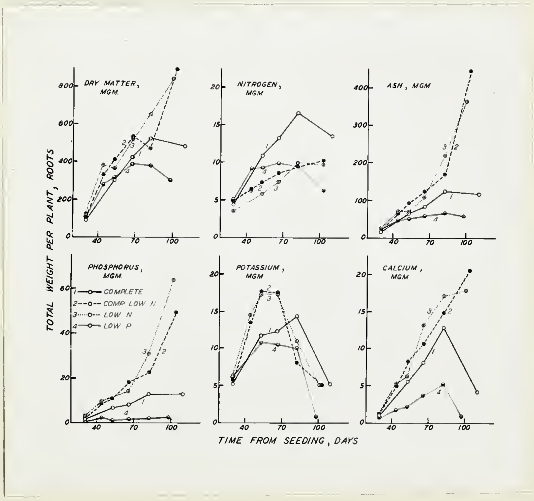


Fig. 14. Total weight in roots.

The chemical composition of vegetative parts of the first four collections and the vegetative parts and grain of the last two collections are presented, as a percentage of the dry matter, in Table XVII. The composition of the roots of all collections is shown in Table XVIII.

The complete results for Collection 1 indicate the magnitude of the experimental error. Cultures one and two at the time of the first collection were of the same constitution, yet the composition of the same variety grown in them varied considerably. It is doubtful whether the method of experimentation used was sufficiently accurate to determine varietal differences.

## Relationship Between Nitrate and Phosphate Absorption.

The total weight results, represented by those for Marquis (Fig. 13 and 14) show that the limitation of nitrogen caused a decrease in yield and a decrease in the absorption of all nutrients except phosphorus.

Table XIX shows that total phosphorus in the vegetative parts of the plants limited in nitrogen was lower than in the controls, but that the weight in the roots was very definitely higher. The total phosphate absorption by the whole plant was slightly higher in the limited nitrogen cultures.

## TABLE XVIII

### Constituents as percentage of dry matter in roots

| Constituent | Collection | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | I | | | II | | | III | | | IV | | | V | | | VI | | |
| | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis |
| **Dry weight** | | | | | | | | | | | | | | | | | | |
| per plant | | | | | | | | | | | | | | | | | | |
| 1 | 0.11 | 0.10 | 0.09 | 0.32 | 0.29 | 0.40 | 0.35 | 0.39 | 0.30 | 0.42 | 0.50 | 0.42 | 0.35 | 0.51 | 0.52 | 0.28 | 0.37 | 0.48 |
| 2 | 0.10 | 0.11 | 0.10 | 0.34 | 0.34 | 0.33 | 0.41 | 0.42 | 0.41 | 0.54 | 0.54 | 0.53 | 0.60 | 0.58 | 0.47 | 0.42 | 0.50 | 0.94 |
| 3 | 0.12 | 0.15 | 0.11 | 0.27 | 0.37 | 0.38 | 0.34 | 0.32 | 0.36 | 0.36 | 0.47 | 0.52 | 0.44 | 0.47 | 0.65 | 0.39 | 0.34 | 0.84 |
| 4 | | | 0.12 | | | 0.28 | | | 0.31 | | | 0.39 | | | 0.38 | | | 0.30 |
| **Nitrogen** | | | | | | | | | | | | | | | | | | |
| 1 | 4.10 | 4.18 | 4.91 | 4.14 | 3.64 | 4.28 | 3.71 | 3.60 | 3.59 | 3.10 | 3.56 | 3.12 | 2.68 | 3.46 | 3.18 | 2.34 | 2.67 | 2.80 |
| 2 | 4.24 | 4.32 | 4.85 | 1.81 | 2.15 | 1.98 | 1.97 | 2.09 | 1.79 | 1.59 | 1.90 | 1.60 | 1.63 | 1.75 | 1.36 | 1.48 | 1.46 | 1.08 |
| 3 | 2.25 | 2.22 | 3.22 | 1.59 | 1.60 | 1.68 | 1.72 | 1.91 | 1.62 | 1.76 | 1.55 | 1.40 | 1.58 | 1.48 | 1.51 | 1.49 | 1.48 | 1.14 |
| 4 | | | 4.13 | | | 3.30 | | | 2.95 | | | 2.48 | | | 2.47 | | | 2.11 |
| **Ash** | | | | | | | | | | | | | | | | | | |
| 1 | 16.8 | 16.7 | 18.6 | 16.3 | 14.7 | 20.3 | 20.3 | 18.6 | 21.5 | 19.7 | 20.0 | 19.8 | 22.3 | 25.0 | 23.9 | 26.3 | 26.3 | 24.2 |
| 2 | 17.6 | 14.6 | 19.6 | 14.6 | 14.6 | 19.9 | 17.6 | 19.9 | 22.2 | 21.7 | 24.5 | 23.3 | -- | 29.2 | 35.8 | 36.9 | 40.1 | 47.4 |
| 3 | 18.6 | 15.8 | 20.4 | 15.4 | 17.5 | 17.8 | 18.9 | 19.2 | 18.8 | 23.9 | 25.6 | 20.9 | 25.7 | 27.2 | 33.7 | 40.0 | 40.9 | 43.2 |
| 4 | | | 18.4 | | | 17.2 | | | 15.9 | | | 15.1 | | | 17.6 | | | 19.7 |
| **Phosphorus** | | | | | | | | | | | | | | | | | | |
| 1 | 2.08 | 1.89 | 1.71 | 2.07 | 1.97 | 1.91 | 1.95 | 1.81 | 2.24 | 2.27 | 1.80 | 2.00 | 2.61 | 2.55 | 2.53 | 3.38 | 2.45 | 2.73 |
| 2 | 2.39 | 1.46 | 1.63 | 2.38 | 1.83 | 2.75 | 2.20 | 2.93 | 2.80 | 2.89 | 3.70 | 3.45 | -- | 4.53 | 4.83 | 6.24 | 7.02 | 5.82 |
| 3 | 2.68 | 2.26 | 2.63 | 2.17 | 2.24 | 2.46 | 2.27 | 2.61 | 2.43 | 2.87 | 3.58 | 2.68 | 3.98 | 3.97 | 4.75 | 6.84 | 6.87 | 7.91 |
| 4 | | | 0.70 | | | 0.74 | | | 0.41 | | | 0.42 | | | 0.42 | | | 0.67 |
| **Potassium** | | | | | | | | | | | | | | | | | | |
| 1 | 6.12 | 5.68 | 5.85 | 4.16 | 3.66 | 4.95 | 3.41 | 3.72 | 3.91 | 2.48 | 3.84 | 2.91 | 2.83 | 2.53 | 2.77 | 0.92 | 0.66 | 1.09 |
| 2 | 6.42 | 5.81 | 5.84 | 1.46 | 2.63 | 4.08 | 1.28 | 2.55 | 4.31 | 1.65 | 4.09 | 3.31 | -- | 1.64 | 1.72 | 0.26 | 0.25 | 0.54 |
| 3 | 5.56 | 4.57 | 5.58 | 3.62 | 3.15 | 3.83 | 3.73 | 3.49 | 4.79 | 3.56 | 2.51 | 3.34 | 1.54 | 1.82 | 1.69 | 0.44 | 0.35 | 0.60 |
| 4 | | | 5.32 | | | 3.99 | | | 3.24 | | | 2.70 | | | 2.62 | | | 0.28 |
| **Calcium** | | | | | | | | | | | | | | | | | | |
| 1 | 1.41 | 1.23 | 1.12 | 1.45 | 1.13 | 1.42 | 1.83 | 1.90 | 1.85 | 2.13 | 1.82 | 1.92 | 2.85 | 2.43 | 2.49 | 0.82 | 0.69 | 0.85 |
| 2 | 1.57 | 1.24 | 1.16 | 1.68 | 1.49 | 1.51 | 2.39 | 2.79 | 2.04 | 2.71 | 2.92 | 2.82 | -- | 4.03 | 2.26 | 1.70 | 1.88 | 2.18 |
| 3 | 1.46 | 1.34 | 1.43 | 1.45 | 1.65 | 1.39 | 1.40 | 2.09 | 1.77 | 3.66 | 3.17 | 2.51 | -- | 4.12 | 2.63 | 1.76 | 1.68 | 2.12 |
| 4 | | | 0.68 | | | 0.58 | | | 0.73 | | | 0.94 | | | 1.25 | | | 0.30 |
| **Magnesium** | | | | | | | | | | | | | | | | | | |
| 1 | 0.32 | 0.22 | 0.26 | 1.32 | 0.23 | 0.24 | 0.33 | 0.23 | 0.29 | 0.30 | 0.29 | 0.33 | 0.36 | 0.28 | -- | 0.50 | 0.21 | 0.27 |
| 2 | 0.43 | 0.35 | 0.40 | 0.28 | 0.19 | 0.24 | 0.39 | 0.20 | 0.19 | 0.22 | 0.18 | 0.18 | -- | 0.06 | 0.52 | 0.39 | 0.29 | 0.74 |
| 3 | 0.25 | 0.18 | 0.33 | 0.32 | 0.20 | 0.19 | 0.35 | 0.27 | 0.18 | 0.18 | 0.16 | 0.19 | 0.16 | 0.08 | 1.01 | 0.27 | 0.35 | 0.94 |
| 4 | | | 0.72 | | | 0.32 | | | 0.31 | | | 0.20 | | | 0.34 | | | 0.34 |

## TABLE XVII

Constituents as a percentage of dry matter in the vegetative parts

| Constituent | Collections | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Vegetative parts | | | | | | | | | | | | | | | | | | Grain | | | | | |
| | I | | | II | | | III | | | IV | | | V | | | VI | | | V | | | VI | | |
| | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis | Reward | Red Bobs | Marquis |
| **Dry weight per Plant.** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 0.49 | 0.60 | 0.38 | 2.25 | 2.83 | 1.26 | 3.22 | 5.19 | 2.63 | 5.06 | 5.20 | 4.65 | 3.50 | 5.78 | 6.80 | 4.08 | 6.03 | 4.97 | 2.04 | 1.76 | 1.27 | 1.83 | 2.40 | 2.08 |
| 2 | 0.59 | 0.60 | 0.35 | 1.72 | 2.07 | 1.10 | 3.40 | 3.37 | 1.73 | 4.82 | 4.95 | 3.93 | 2.81 | 3.64 | 5.28 | 3.51 | 4.41 | 3.74 | 1.47 | 1.39 | 0.77 | 1.84 | 2.10 | 1.83 |
| 3 | 0.49 | 0.34 | 0.30 | 1.28 | 1.24 | 1.09 | 2.73 | 1.95 | 1.59 | 3.79 | 2.70 | 3.44 | 2.01 | 2.23 | 3.33 | 2.78 | 2.49 | 2.80 | 1.14 | 1.07 | 0.83 | 1.43 | 1.27 | 1.52 |
| 4 | | | 0.25 | | | 0.68 | | | 1.26 | | | 2.28 | | | 2.55 | | | 2.03 | | | 0.69 | | | 0.88 |
| **Nitrogen** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 5.05 | 4.98 | 5.36 | 3.38 | 3.39 | 4.33 | 3.27 | 3.48 | 3.78 | 3.07 | 3.06 | 2.70 | 1.16 | 2.12 | 2.22 | 1.04 | 1.68 | 1.50 | 3.31 | 2.64 | 2.99 | 3.97 | 3.73 | 3.89 |
| 2 | 4.89 | 5.06 | 5.50 | 1.76 | 1.86 | 1.91 | 1.62 | 1.71 | 1.41 | 1.00 | 1.15 | 1.05 | 0.56 | 0.83 | 0.69 | 0.31 | 0.33 | 0.29 | 1.97 | 1.97 | 1.90 | 2.45 | 2.48 | 2.37 |
| 3 | 2.58 | 2.51 | 3.92 | 1.22 | 1.35 | 1.53 | 1.17 | 1.19 | 1.62 | 1.00 | 1.01 | 1.16 | 0.57 | 0.82 | 0.90 | 0.28 | 0.30 | 0.32 | 2.40 | 2.08 | 1.99 | 2.81 | 2.71 | 2.55 |
| 4 | | | 5.36 | | | 2.88 | | | 2.64 | | | 1.90 | | | 1.46 | | | 1.00 | | | 3.23 | | | 4.05 |
| **Ash** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 19.5 | 15.1 | 15.7 | 14.1 | 14.1 | 18.4 | 9.5 | 11.3 | 12.4 | 8.7 | 13.9 | 12.1 | 7.7 | 8.5 | 9.4 | 9.3 | 11.5 | 11.0 | 2.50 | 2.51 | 2.95 | 2.70 | 2.72 | 2.82 |
| 2 | 19.1 | 15.4 | 16.8 | 8.3 | 10.7 | 12.8 | 5.7 | 7.0 | 9.6 | 5.3 | 7.0 | 8.1 | 5.3 | 6.1 | 6.5 | 6.2 | 6.5 | 8.9 | 2.37 | 2.31 | 2.53 | 2.40 | 2.43 | 2.79 |
| 3 | 16.3 | 13.6 | 16.0 | 9.1 | 10.3 | 12.8 | 7.1 | 7.2 | 9.1 | 6.5 | 7.4 | 8.5 | 6.2 | 7.6 | 6.9 | 7.5 | 7.9 | 8.6 | 2.40 | 2.56 | 2.64 | 2.39 | 2.49 | 2.49 |
| 4 | | | 15.0 | | | 14.1 | | | 9.1 | | | 9.6 | | | 8.0 | | | 8.6 | | | 2.16 | | | 1.69 |
| **Phosphorus** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 0.81 | 0.96 | 1.12 | 0.50 | 0.49 | 0.63 | 0.42 | 0.56 | 0.60 | 0.32 | 0.53 | 0.39 | 0.31 | 0.43 | 0.39 | 0.16 | 0.34 | 0.26 | 0.56 | 0.53 | 0.63 | 0.64 | 0.63 | 0.70 |
| 2 | 1.00 | 1.01 | 1.41 | 0.46 | 0.43 | 0.69 | 0.42 | 0.46 | 0.64 | 0.32 | 0.33 | 0.36 | 0.28 | 0.33 | 0.42 | 0.29 | 0.28 | 0.41 | 0.55 | 0.46 | 0.54 | 0.55 | 0.57 | 0.70 |
| 3 | 1.07 | 1.00 | 1.58 | 0.38 | 0.45 | 0.65 | 0.34 | 0.36 | 0.61 | 0.30 | 0.34 | 0.30 | 0.26 | 0.39 | 0.36 | 0.29 | 0.38 | 0.36 | 0.55 | 0.51 | 0.55 | 0.56 | 0.57 | 0.67 |
| 4 | | | 0.36 | | | 0.17 | | | 0.12 | | | 0.09 | | | 0.05 | | | 0.02 | | | 0.35 | | | 0.29 |
| **Potassium** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 7.27 | 6.96 | 7.33 | 4.79 | 4.77 | 6.44 | 4.14 | 5.01 | 5.48 | 2.72 | 4.49 | 3.99 | -- | 3.71 | 3.95 | 3.70 | 4.40 | 4.05 | 0.66 | 0.66 | 0.83 | 0.58 | 0.60 | 0.62 |
| 2 | 7.89 | 7.18 | 7.69 | 2.66 | 3.62 | 4.52 | 2.05 | 2.88 | 3.97 | 1.45 | 2.09 | 2.62 | 1.84 | 2.45 | 2.50 | 1.97 | 2.48 | 3.03 | 0.64 | 0.63 | 0.84 | 0.53 | 0.58 | 0.54 |
| 3 | 7.24 | 5.92 | 7.19 | 3.00 | 3.43 | 4.13 | 2.66 | 2.87 | 3.58 | 1.87 | 2.21 | 2.55 | 2.55 | 2.79 | 2.70 | 2.84 | 2.91 | 3.10 | 0.62 | 0.74 | 0.79 | 0.55 | 0.58 | 0.54 |
| 4 | | | 7.49 | | | 4.65 | | | 4.17 | | | 2.81 | | | 3.41 | | | 3.49 | | | 0.71 | | | 0.46 |
| **Calcium** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 0.57 | 0.56 | 0.65 | 0.45 | 0.39 | 0.55 | 0.40 | 0.42 | 0.47 | 0.37 | 0.41 | 0.41 | -- | 0.76 | 0.48 | 0.72 | 0.98 | 0.62 | 0.09 | 0.07 | 0.08 | 0.09 | 0.09 | 0.08 |
| 2 | 0.73 | 0.55 | 0.72 | 0.43 | 0.31 | 0.43 | 0.40 | 0.31 | 0.37 | 0.34 | 0.31 | 0.31 | 0.47 | 0.36 | 0.33 | 0.60 | 0.43 | 0.53 | 0.07 | 0.07 | 0.07 | 0.09 | 0.06 | 0.15 |
| 3 | 0.63 | 0.53 | 0.61 | 0.28 | 0.32 | 0.41 | 0.27 | 0.30 | 0.37 | 0.24 | 0.28 | 0.33 | 0.31 | 0.35 | 0.38 | 0.44 | 0.54 | 0.76 | 0.07 | 0.06 | 0.09 | 0.06 | 0.06 | 0.14 |
| 4 | | | 0.67 | | | 0.45 | | | 0.38 | | | 0.34 | | | 0.47 | | | 0.65 | | | 0.09 | | | 0.07 |
| **Magnesium** | | | | | | | | | | | | | | | | | | | | | | | | |
| 1 | 0.18 | 0.24 | 0.28 | 0.17 | 0.15 | 0.22 | 0.15 | 0.17 | 0.20 | 0.13 | 0.17 | 0.16 | 0.14 | 0.15 | 0.15 | 0.17 | 0.24 | 0.17 | 0.18 | 0.18 | 0.20 | 0.20 | 0.21 | 0.23 |
| 2 | 0.15 | 0.23 | 0.28 | 0.15 | 0.12 | 0.15 | 0.10 | 0.11 | 0.15 | 0.13 | 0.10 | 0.12 | 0.14 | 0.15 | 0.10 | 0.16 | 0.12 | 0.17 | 0.19 | 0.18 | 0.20 | 0.20 | 0.18 | 0.22 |
| 3 | 0.10 | 0.15 | 0.23 | 0.10 | 0.12 | 0.13 | 0.10 | 0.12 | 0.15 | 0.07 | 0.11 | 0.16 | 0.06 | 0.13 | 0.11 | 0.11 | 0.14 | 0.15 | 0.18 | 0.19 | 0.21 | 0.19 | 0.20 | 0.21 |
| 4 | | | 0.07 | | | 0.15 | | | 0.09 | | | 0.14 | | | 0.14 | | | 0.20 | | | 0.17 | | | 0.16 |

TABLE XIX

Total absorption of nitrogen and phosphorus, mgm. per plant

| Culture | Nitrogen | | | Phosphorus | | |
|---|---|---|---|---|---|---|
| | Roots | Tops | Total | Roots | Tops | Total |
| **Reward** | | | | | | |
| 1 | 6.6 | 115.1 | 121.7 | 9.5 | 18.0 | 27.5 |
| 2 | 6.2 | 56.0 | 62.2 | 26.2 | 20.4 | 46.6 |
| 3 | 5.8 | 48.0 | 53.8 | 26.7 | 16.0 | 42.7 |
| **Red Bobs** | | | | | | |
| 1 | 9.9 | 190.8 | 200.7 | 9.1 | 35.5 | 44.6 |
| 2 | 7.3 | 67.1 | 64.4 | 35.1 | 24.4 | 59.5 |
| 3 | 5.0 | 42.5 | 47.5 | 23.4 | 16.9 | 40.3 |
| **Marquis** | | | | | | |
| 1 | 13.4 | 155.5 | 168.9 | 27.6 | 13.1 | 40.7 |
| 2 | 10.2 | 53.9 | 64.1 | 28.1 | 49.5 | 77.6 |
| 3 | 9.6 | 47.8 | 57.4 | 20.2 | 64.2 | 84.4 |
| 4 | 6.3 | 56.1 | 62.4 | 3.0 | 2.0 | 5.0 |

Limitation of nitrogen did not increase the percentage of phosphorus in the vegetative parts or the grain (Table XVII). The percentages in the low nitrogen cultures of Reward and Red Bobs were in general slightly lower than in the complete, while the percentages in the low nitrogen cultures of Marquis were approximately the same as in the complete for all except the last collection when they were definitely higher.

The results of the chemical analyses of the roots (Table XVIII and Fig. 14) showed that there was more phosphorus in the roots grown in the limited nitrogen cultures, and that phosphorus as a percentage of dry matter

was definitely higher in these roots. At the time of the last collection the percentage of phosphorus in the roots of all low nitrogen cultures was more than twice as high as in the roots grown in complete culture. This difference was even greater in the weights of total phosphorus (Fig. 14).

The results show that the nitrogen limitations used in these experiments caused a definite decrease in yield and a very large increase in the absorption of phosphate by the roots which was not translocated to the vegetative parts of the plant.

The limitation of phosphorus caused a much greater decrease in yield than the limitation of nitrogen and a correspondingly greater decrease in the absorption of all nutrients. The absorption of nitrogen was markedly decreased and the percentage of nitrogen in the vegetative parts and roots was very much lower than in the complete culture plants. The percentage in the grain was, however, increased.

This higher concentration of nitrogen in the grain is in agreement with Hoagland's results (11), but it is probably not due to the same cause. In Hoagland's experiments the phosphorus supply was not altered until quite late in the development of the plant, and then it was stopped completely. In this experiment phosphorus was limiting throughout growth and must, from its effect on yield, have markedly upset many of the metabolic processes

of the plant. The higher concentration of nitrogen in the grain is probably a very indirect effect of the low phosphorus supply, and is no real indication of a relationship between nitrate and phosphate absorption.

## Culture 2 in Relation to Fallis Soil Conditions.

The supply of nitrogen in culture 2 (complete:low N) was planned to be similar to the supply of nitrogen in the Fallis soils. Analyses of the plants grown at Fallis showed that 37% of the total nitrogen absorbed was absorbed in the first month. The composition of culture 2 was so arranged that plants grown in it also absorbed 37% of the total available nitrogen in the first month of growth. Results in the first part of this paper also indicated that phosphorus was at all times readily available in the Fallis soil. The phosphorus supply in culture 2 was much in excess of the needs of the plant.

It may be assumed then that the supply of nitrogen and phosphorus in culture 2 was somewhat similar to the nitrogen and phosphorus supply in the Fallis soil. Comparison of the chemical analyses of the plants grown in culture 2 and on Fallis soil should therefore indicate the importance of the nitrogen-phosphorus relationship in controlling the composition of the Fallis plants.

In order to make such a comparison it was necessary to have some control with which to compare the composition of the Fallis plants, and Edmonton plants

have been used. The Edmonton soil has, however, been shown to respond to phosphate fertilizer and may be limiting in this element.

Plants grown in culture 2 fail to show the increase in the percentage of phosphorus noted under Fallis conditions. These plants were lower in all constituents than the control, but the smallest differences were in the percentages of phosphorus and magnesium.

One of the important differences between the composition of the Fallis and Edmonton plants was that the Fallis grain was much richer in all constituents. This difference did not exist between culture 2 and culture 1 (complete). The grain grown in culture 2 was definitely lower in all constituents than the grain grown in the complete culture. This greater concentration of nutrients in the Fallis grain was brought about by a greatly increased translocation of nutrients to the grain. There was also a greater translocation of some nutrients in the plants grown in culture 2 as the following Table XX shows, but the increase was not as great as it was at Fallis, nor was it sufficient to raise the percentage composition of the grain above that of the control. Table XX shows that there was a much greater percentage translocation of phosphorus and magnesium under field conditions.

### TABLE XX

Constituents in grain of mature plants expressed as a percentage of the total constituents

| | Dry matter | Nitrogen | Ash | Phosphorus | Potassium | Calcium | Magnesium |
|---|---|---|---|---|---|---|---|
| Marquis | | | | | | | |
| Complete | 29.5 | 66.0 | 10.5 | 52.5 | 6.0 | 5.1 | 36.2 |
| Complete: low N | 32.9 | 84.1 | 13.3 | 45.5 | 8.0 | 12.0 | 38.7 |
| Reward | | | | | | | |
| Complete | 31.0 | 72.4 | 11.5 | 64.7 | 6.5 | 5.0 | 25.6 |
| Complete: low N | 34.4 | 80.4 | 16.9 | 49.7 | 12.3 | 7.4 | 40.9 |
| Edmonton | 33.6 | 73.2 | 10.4 | 78.2 | 15.1 | 6.7 | 63.6 |
| Fallis | 31.8 | 74.4 | 11.0 | 62.7 | 22.4 | 17.9 | 65.9 |
| Red Bobs | | | | | | | |
| Complete | 28.5 | 64.0 | 8.6 | 42.3 | 5.1 | 3.5 | 34.4 |
| Complete: low N | 32.3 | 78.4 | 15.1 | 48.9 | 10.0 | 6.3 | 39.6 |
| Edmonton | 34.8 | 72.4 | 11.4 | 78.5 | 15.1 | 6.7 | 63.6 |
| Fallis | 36.7 | 79.5 | 15.7 | 73.0 | 30.2 | 23.1 | 75.0 |

Table XXI gives the nitrogen:phosphorus ratios in the plants of Reward and Red Bobs grown in cultures 1 and 2 and at Edmonton and Fallis at progressive stages of maturity. The ratios for the plants grown in culture 2 and on Fallis soil were very much alike. Ratios for plants grown in culture 1 were, however, lower than corresponding ratios for the Edmonton plants. This is indication that phosphorus was less available at Edmonton than in the complete culture.

### TABLE XXI

The relation between nitrogen and phosphorus

| Variety | Culture or soil | Collections | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 |
| Reward | 1 | 7.89 | 8.38 | 9.78 | 10.3 | 6.30 | 7.47 |
| | 2 | 6.74 | 3.88 | 4.57 | 3.08 | -- | 2.26 |
| Red Bobs | 1 | 7.54 | 9.26 | 9.04 | 8.20 | 6.69 | 7.61 |
| | 2 | 7.76 | 5.09 | 4.05 | 3.12 | 2.56 | 1.82 |
| Reward | Edmonton | 9.57 | 11.4 | 9.80 | 8.96 | 9.89 | -- |
| | Fallis | 7.84 | 3.72 | 3.50 | 2.97 | 3.26 | -- |
| Red Bobs | Edmonton | 11.0 | 10.6 | 10.7 | 7.96 | 8.25 | -- |
| | Fallis | 6.59 | 4.12 | 3.48 | 3.43 | 3.26 | -- |

These comparisons indicate that the nitrogen phosphorus relationship in the Fallis soil was not alone responsible for the high phosphorus content of the Fallis plants. The failure of the plants grown in low nitrogen cultures to translocate the high accumulation of phosphorus in the roots to the vegetative parts is important. A correspondingly high accumulation of calcium suggested that perhaps the phosphorus was precipitated in the roots as calcium phosphate. Further experiments are, however, being carried out to determine the effect of limiting other nutrients beside nitrogen on the accumulation of phosphorus in the plant.

## Conclusions

1. The limitations of nitrogen caused a definite decrease in yield and a decrease in the absorption of all nutrients studied except phosphorus. There was a very large increase in the absorption of phosphate by the roots, but it was not translocated to the grain.

2. The limitation of phosphorus caused a much greater decrease in yield than the limitations of nitrogen and a correspondingly greater decrease in the absorption of all nutrients. The percentage of nitrogen in the vegetative parts and roots was much lower than in the control plants, but the percentage in the grain was slightly higher.

3. A comparison of the composition of the plants grown in culture 2 and those grown on the Fallis soil indicated that the nitrogen-phosphorus relationship was not alone responsible for the high percentage of phosphorus in the Fallis plants.

## GENERAL SUMMARY

The results reported are only of a preliminary nature, and it is impossible to draw any definite conclusions from them with regard to the relation between the nutrition of the wheat plant and its effect on wheat quality or the ability of the flour milled from the wheat to keep on storage.

The percentage of protein in the grain, which is related to the absorption of nitrogen by the whole plant, is known to be highly correlated with wheat quality, and undoubtedly the ability of the varieties to accumulate nitrogen in the grain when grown under the two soil conditions was the greatest factor in determining the quality of the wheat produced. Other factors must, however, be important in determining many of the physical properties of the grain proteins and the changes in these properties which accompany flour storage.

There were definite differences in the absorption of nutrients by the two varieties growing on both soils, but further experimentation is necessary before it can be stated whether these differences are responsible for the known differences in the quality and keeping properties of the flour milled from these varieties. Nitrogen, phosphorus and sulphur are undoubtedly very important in determining the nature of the proteins and the baking quality of the flour, and it may be the upset

in the balance of these constituents in the Fallis grain that is particularly important; but many of the other elements, particularly those that occur only in small quantities and act in the role of catalysts, may be just as important.

The composition of the plants at progressive stages of development have shown that there are clear cut differences between the absorption of the two varieties and the reaction of the varieties to two very different soil types. This type of result, which elucidates the factors of yield and grain composition, should be of particular importance in the evaluation of varieties by the plant breeder.

The results also indicate clearly the availability of the important nutrients in the two soils and suggest various fertilizer practices. It is only by the use of studies of this nature, which determine the availability of nutrients in the soil at all stages in the life cycle of the plant, that accurate scientific calculations of the fertilizer requirements of a soil can be made.

As far as the writer is aware, the experiments on the phosphorus composition of the developing grain are more comprehensive than any previously reported. The changes in the nitrogen content have been studied in much detail by previous workers, and it has been suggested that phosphorus varies in a manner similar to nitrogen. The results reported in this paper are in general agreement

with the previous work on phosphorus distribution in wheat and other seeds. Phytin is the main storage form of phosphorus and accumulates as the grain matures due to the transport of phosphorus from the vegetative parts of the plant and the break down of other phosphorus compounds in the grain. The results also show that the percentage of phosphorus in the proteins and closely related compounds was higher in the earlier stages of the grain's development and decreased with the formation of the gluten proteins.

The nutrient culture experiments failed to show an accumulation of phosphorus in the plants grown with a limited supply of nitrogen. The reason for this failure is as yet unknown. Various possibilities suggest themselves. It may have been due to the degree or method of limitation of the nitrogen, the pH of the solution, the presence of too high or too low a concentration of other nutrients or any other variable of the nutrient culture solution. Further experiments are being planned to investigate the action of decreasing the pH of the solution and lowering the concentration of sulphur and calcium.

## ACKNOWLEDGEMENTS

The writer sincerely thanks Dr. A. G. McCalla for his advice and encouragement during the progress of this investigation, Dr. J. W. Hopkins for advice on the statistical interpretation of the results and the members

of the cereal laboratory staff for their help with much of the routine chemical analyses.

The experiments were made possible by a research scholarship from the University of Alberta and a grant from the National Research Council of Canada.

## REFERENCES

1. AAMODT, O.S. and McCALLA, A.G. Quality and keeping properties of flour from wheat grown on the black and gray soils of Alberta. Can. J. Research C.13:160-167. 1935.
2. ANDREWS, J.S. and BAILEY, C.H. Distribution of organic phosphorus in wheat. J. Indus. and Eng. Chem. 24:80-82. 1932.
3. AVERILL, H.P. and KING, C.G. The phytin content of foodstuffs. J. Am. Chem. Soc. 48:724-728. 1926.
4. BAILEY, C.H. The Chemistry of Wheat Flour. Chemical Catalog Co., New York. 1935.
5. BAYFIELD, E.G. Soft winter wheat studies. III. The effect of some factors influencing viscosity and protein. Cereal Chem. 12:1-15. 1935.
6. DEMOLON, M.A. Sur le chimisme comparé des variétés de blé. Compt. Rend. Acad. Agric., France 14:591-593. 1935.
7. DeTURK, E.E., HOLBERT, J.R. and HAWK, B.W. Chemical transformation of phosphorus in the growing corn plant, with results on two first generation crosses. J. Agric. Research 46:121-141. 1933.
8. FISHER, R.A. Statistical Methods for Research Workers. Oliver and Boyd, Edinburgh. 1932.
9. GERICKE, W.F. Bread quality of wheat produced in aqueous culture media. Science 77:229-232. 1933.
10. HARRIS, R.S. and MOSHER, L.M. Estimation of phytin phosphorus. Ind. Eng. Chem. (Anal. Ed.) 6:320-321. 1934.

11. HOAGLAND, D.R. Private communication. 1935.

12. HIBBARD, P.S. and STOUT, P.R. Determination of potassium. J. Assoc. Official Agric. Chem. 16: 137-140. 1933.

13. KNOWLES, F. and WATKIN, J.E. The assimilation and translocation of plant nutrients in wheat during growth. J. Agric. Sci. 21:612-637. 1931.

14. KRAYBILL, H.R. Plant metabolism studies as an aid in determining fertilizer requirements. Ind. and Eng. Chem. 22:275-276. 1930.

15. KRÜGEL, C., DREYSPRUNG, C. and KURTH, H. Der Einfluss der phosphorsäure dungung auf den Ertag und du qualität von Braugersten. Zeits. fur Pflanz. B.21:12-32. 1933.

16. MARSH, R.S. Preliminary studies on the sulphur content of the tomato. Amer. Soc. Hort. Sci. Proc. 19:83-84. 1922.

17. MATHER, T.H. The effect of fertilizers upon the forms of phosphorus and the amounts of phosphorus, nitrogen and silica in hays. Sci. Agric. 11:35-63. 1929.

18. MAUME, L. and DULAC, J. Différences variétables dans l'absorption de l'acide phosphorique et de la potasse par des blés ayent atteint une même époque physiologique dans un même milieu. Compt. Rend. Acad. Sci. 198:199-202. 1934.

19. ____________________. Role important du milieu (climat et sol) dans l'absorption de N, $P_2O_5$, $K_2O$ par des blés ayant atteint une même époque physiologique. Compt. Rend. Acad. Agr. France 21:120-123. 1935.

20. McCALLA, A.G. The effect of nitrogen nutrition on the protein and non-protein nitrogen of wheat. Can. J. Research 9:542-570. 1933.

21. MICHEL-DURAND, E. Sur le métabolisme du phosphore dans les feuilles du gui. Compt. Rend. Acad. Sci. Paris 199:1653-1655. 1934.

22. NEWTON, J.D. The fertilizing value of sulphate in natural "alkali" for gray wooded soils. Sci. Agric. 17:241-244. 1936.

23. NEWTON, R. and McCALLA, A.G. Effect of frost on wheat at progressive stages of maturity. III. Milling and baking quality. Can. J. Research C.13:263-282. 1935.

24. PETERS, J.P. and VAN SLYKE, D.P. Quantitative clinical chemistry volume. II. Methods. The Williams and Wilkins Co., Baltimore. 1932.

25. PROEBSTING, E.L. and KINMAN, C.F. Orchard trials of nitrogen and phosphorus. Proc. Amer. Soc. Hort. Sci. 30:426-430. 1930.

26. PULCHER, G.W., LEAVENWORTH, C.S. and VICKENY, H.B. Determination of total nitrogen of plant extracts in presence of nitrates. Ind. Eng. Chem. (Anal. Ed.) 2:191-193. 1930.

27. RICHARDS, M.B. and GODDEN, W. The Pemberton Neumann method for the estimation of phosphorus. The Analyst 49:565-572. 1924.

28. ROUSSEAUX, E. and SIROT, M. Les matieres azotees et l'acide phosphorique dans le maturation et la germination du ble. Compt. Rend. Acad. Sci. 171:578-580. 1920.

29. SANDO, C.E. Lipides and their estimation in vegetable tissues. Plant Physiol. 3:155-184. 1928.

30. SCHRUMPF-PIERRON, P. Effet du facteur "variété" sur l'équilibre mineral des blés. Compt. Rend. Soc. Biol. 111:846-848. 1932.

31. SINCLAIR, A.T. M.Sc. thesis, University of Alberta. 1936.

32. THOMAS, W. Absorption, utilization and recovery of nitrogen, phosphorus and potassium by apple trees grown in cylinders and subject to differential treatment with nutrient salts. J. Agric. Research 47:565-581. 1933.

33. TIPPET, L.H.C. Tracts for Computers. 15. Random Sampling Numbers. Cambridge University Press, London. 1927.

34. TRUOG, EMIL and MEYER, A.H. Improvements in the Deniges Colorimetric method for phosphorus and arsenic. Ind. Eng. Chem. (Anal. Ed.) 1:136-146. 1929.

35. WOIKOFF, M.I. Determination of sulphur. Soil Sci. 18:371-377. 1924.

36. WOOD, J.B. The chemistry of strength of wheat flour. II. The shape of the loaf. J. Agric. Sci. 2:267-277. 1907.

37. WOODMAN, H.E. and ENGLEDOW, F.L. A chemical study of the development of the wheat grain. J. Agric. Sci. 14:563-586. 1924.

38. WORKING, EARL B. Some oxidizing effects of flour bleaching. Cereal Chem. 5:431-435. 1928.

39. WYATT, F.A. and NEWTON, J.D. Wooded soils and their management. Univ. of Alberta, Coll. Agric. Bull. 21. 1932.

B29744